The relative importance of local and landscape scale factors to chalk grassland butterflies

Thesis

The Relative Importance of Local and Landscape Scale Factors to Chalk Grassland Butterflies

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ABSTRACT

The relative importance of habitat and landscape for chalk grassland butterflies was investigated among a network of chalk grassland habitat patches. Local scale habitat selection models were derived from analyses on a single large chalk grassland site (Porton Down). Landscape scale models were then derived from species-specific local scale variables added to variables measured in the patch network, which included Porton Down as a major source site. An investigation was also carried out as to whether landscape scale processes were acting within Porton Down.

Models showed that landscape scale processes may be acting within the single, large site for some species. However, lack of patch definition and natural variations in local population densities may give rise to apparent landscape scale processes within this site which fundamentally differ from true landscape scale processes.

At the true landscape scale across the patch network, patch area was the most commonly included landscape scale variable in models, although only for five species. For one species, dark green fritillary *Argynnis aglaja*, distance from the major source site and average distance from other sites were of over-riding importance. For most species, local scale habitat and environment variables were sufficient to describe their presence or density among the patch network.

Incidence Function Models were used to estimate metapopulation dynamic parameters for seven species. Both sensitivity to environmental stochasticity and colonisation ability

were correlated with species' scores on canonical community analysis axes (related to local habitat, patch area, distance from source site and inter-patch distance measures). This suggests that species conforming to conventional metapopulation models form an ecological continuum with those responding to local scale habitat and landscape scale processes in a less prescriptive fashion.

Species groups with either restricted or widespread distributions appear to conform to a landscape connectivity model. Five ecologically similar species appear to be moving from the former to latter group across a 'connectivity threshold', possibly due to recent increases in larval food-plant availability in the wider landscape.

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1. INTRODUCTION

1.1 HISTORICAL OVERVIEW OF INVERTEBRATE POPULATION ECOLOGY

The study of animal populations has tended to focus on particular academic hypotheses which have ebbed and flowed in importance. The first emphasis was on the tension between biotic and climatic factors (Uvarov 1931) followed by Nicholson's (1933) argument for regulation by density-dependence. In fact, this latter aspect of population regulation has been a central theme for zoological ecology since Andrewartha and Birch (1954) set it in full context. Detailed analyses of population cycles by workers such as Hassell and Varley (1969) and mortality (*k*-factor) analysis by workers such as Varley and Gradwell (1960) focussed down in an attempt to explain population regulation by rigorous descriptive statistics but, in failing to detect density-dependence, the search for population regulation became something of a holy grail (Cappuccino 1995).

Since the mid-1960s, wider concepts with links to other fields of study or disciplines have become the most tantalizing academic areas of study. Firstly, the island biogeography theories of MacArthur and Wilson (1967), and subsequently, the first author's development of the concept of community ecology (MacArthur 1955) was picked up and developed by a number of leading academics (Kareiva 1989). To a large degree, it was these latter two areas of research which formalized the link between population dynamics and species' natural surroundings, or habitat.

While some topics, such as optimal foraging behaviour theory (Krebs and McCleery 1984), re-focussed energy on autecological research, population dynamics has itself re-

focussed on nonequilibrium dynamics, in which local populations do not inevitably, and more realistically, show a trend towards stable population levels (Murdoch 1994).

1.2 CURRENT THEORETICAL APPROACHES TO INVERTEBRATE POPULATION ECOLOGY

1.2.1 Patterns in Time series

Time series data have often provided the largest data sets for population analysis. However, the statistical means for deriving information from these data have only relatively recently been developed. Comparison between modelled and observed time series is one of the most common methods of analysis. Population regulation can also be revealed by calculating the cumulative variance of natural populations (Murdoch and Walde 1989), where regulated ('bounded') populations show a stabilizing cumulative variance. Population cycles and even chaotic behaviour can be incorporated in this method (Murdoch 1994).

Comparative approaches looking at the relationship between organismal traits such as *r*- and *k*-selected tendencies (Southwood 1981), generalists versus specialists (Watt 1964) and tendency to aggregate (Root and Cappuccino 1992) have all shown to have some bearing on the degree and boundedness of invertebrate population levels over time. For butterflies, analysis of long-term trends has been restricted comparisons across 'experimental blocks' such as relative changes within wood white *Leptidea sinapsis* populations due to changes in ride habitat (Warren 1985).

1.2.2 Other Factors Driving Population Change

1.2.2.1 Predation and Parasitism

Predation and parasitism are clearly very important factors and have been intensively studied in invertebrates (Hassell 1976). In butterflies, anti-predator mechanisms through camouflage and chemical defences are well known (Brakefield *et al* 1992). Parasitism, through predation by parasitoids, is a common and well studied mechanism in insects (Cappuccino 1995). The levels of parasitism observed in butterflies appears to be generally low in most years (Warren 1992), but is now known to be an important driver of metapopulation dynamics in some (e.g. marsh fritillary, Porter 1983) and wider population cycles (e.g. Holly blue *Celastrina argiolus*). Avoidance of parasitoids has been shown to influence habitat selection by ovipositing females (Shaw 1977) and probably has wider, but as yet, unknown consequences on butterfly distributions (Porter *et al* 1992).

1.2.2.2 Dispersal

Dispersal has recently been recognized as arguably the single most important mechanism influencing invertebrate population size and stability (Denno and Peterson 1995). Dispersal as migration is a central tenet in metapopulation theory (see Section 1.2.3) in that colonization rates are intimately dependent on migration rates (Hanski and Kuussaari 1995). Hanski (1999) lists five local factors which are also likely to affect an invertebrates decision to migrate: inbreeding avoidance, sibling competition, resource competition (at high population density), conspecific attraction (at low population density) and escape from imminent extinction.

1.2.2.3 Disease

Disease is a major factor in determining population levels and has been shown to drive the cyclic dynamics of forest lepidoptera (Anderson and May 1980). There is not much evidence that disease plays a major part in regulating temperate butterfly populations except when species which can feed on commercial crops reach pest proportions. Warren (1992) felt that a large proportion of recorded deaths due to predation in life-table studies could actually be attributable to already diseased animals.

1.2.2.4 Maternal Effects

The 'quality' of the individual and therefore collectively the population, may be influenced by the environment of the previous generation. Such a time-lag effect is known to cause fluctuations in population growth (May 1974) and has been termed the maternal effect (Rossiter 1995). Rossiter (1995) has documented five Lepidoptera genera (all moths) where the maternal effect has been recorded, with the best data on the gypsy moth *Lymantria dispar*. In this species, food quality has an immediate effect on the current generation and effects both the ability of survival to reproductive age and fecundity of the subsequent offspring. There is no reason to believe that the maternal effect is not strong among butterfly species, particularly as most are more specialized than the generally polyphagous moths.

1.2.3 Metapopulation Dynamics

The term metapopulation describes a set of local populations that persist in a balance between stochastic local extinctions and establishment of new local populations (Hanski and Gilpin 1991). The concept of a 'metapopulation' was introduced three decades ago (Levins 1970), but linking the concept to models of metapopulation dynamics is a comparatively new area of work. Hanski (1999) lists twelve types of ecological observation which are evidence that metapopulation processes are active in dynamic population ecology. They are:

- Population size or density is significantly affected by migration.
- Population density is affected by patch area and isolation.
- Asynchronous local dynamics make simultaneous extinctions unlikely.
- Population turnover (extinction and re-colonization) is a relatively common occurrence.
- Apparently suitable habitat is often empty.
- Metapopulations persist despite population turnover.
- Extinction risk is related to patch area.
- Colonization rate is related to patch isolation.
- Patch occupancy is related to patch area and isolation.
- Spatially realistic metapopulation models are robust predictors of metapopulation dynamics in any given fragmented landscape.
- Competitors can coexist in dynamic metapopulations.
- Predators and prey can coexist in dynamic metapopulation.

Despite the apparently exacting list of conditions above, metapopulation dynamic models have been constructed and tested for a number of species including the northern spotted owl *Strix occidentalis caurina* (Lande 1988), the Eurasian red squirrel *Sciurus vulgaris* (Andren and Delin 1994) the silver-spotted skipper *Hesperia comma* (Thomas and Jones 1993) and the seminal work on the Glanville fritillary *Melitaea cinxia* by Hanski and his co-workers (Hanski *et al* 1994; Hanski *et al* 1995).

1.3 COMMUNITIES

Despite the fact that butterfly species clearly live together in intimate proximity, there is very little evidence that these are true species associations such as can be found in the constant groupings of plants (Rodwell 1991 *et seq.*). Classification of 'communities' is difficult for butterflies due to constant species changes. These appear to be due to associations with vegetation succession and land-use changes rather than species-species interactions (Porter *et al* 1992).

Intraspecific interactions have been observed in many species. The classic example is the territorial flight behaviour of speckled wood *Pararge aegeria* (Davies 1978). There may also be competition between adults and larvae for food-plants, which has resulted in cannibalism among orange tip *Anthocaris cardamines* larvae (Courtney 1980).

Interspecific interactions can be largely explained by non-competitive factors (Strong *et al* 1984). For example, most larvae competing for food are affected by reductions in food quality and the need to find alternative resources. There is therefore no clear evidence for competitive exclusion (Hutchinson 1959) in British butterflies, but compelling evidence was seen in North America when the European small white *Pieris rapae* was introduced

triggering a subsequent decline in the local race of green-veined white *Pieris napi* which feeds on the same larval food-plant (Shapiro 1975).

Resource partitioning is the final type of community interaction relevant to butterflies and this is discussed in Section 1.4 below.

1.4 HABITAT SELECTION

Owen (1959) and Gilbert and Singer (1975) listed five major niche differences among British butterflies:

1. Larval food (host) plant;
2. Part of host plant used;
3. Phenology and voltinism;
4. Parasite and predator escape mechanisms and behaviour; and
5. Habitat and flowers (nectar sources) visited by adults.

This could have been extended to most, if not all phytophagous insect groups.

Despite this early marker, insect and typically, butterfly habitat requirement studies have historically been largely confined to host food-plant selection in population dynamic studies (see for example Solbreck 1995). Few studies of butterflies have implicitly studied species-specific habitat selection in the wider sense, where the larval food-plant is set in the context of underlying geology and surrounding plant communities and associated

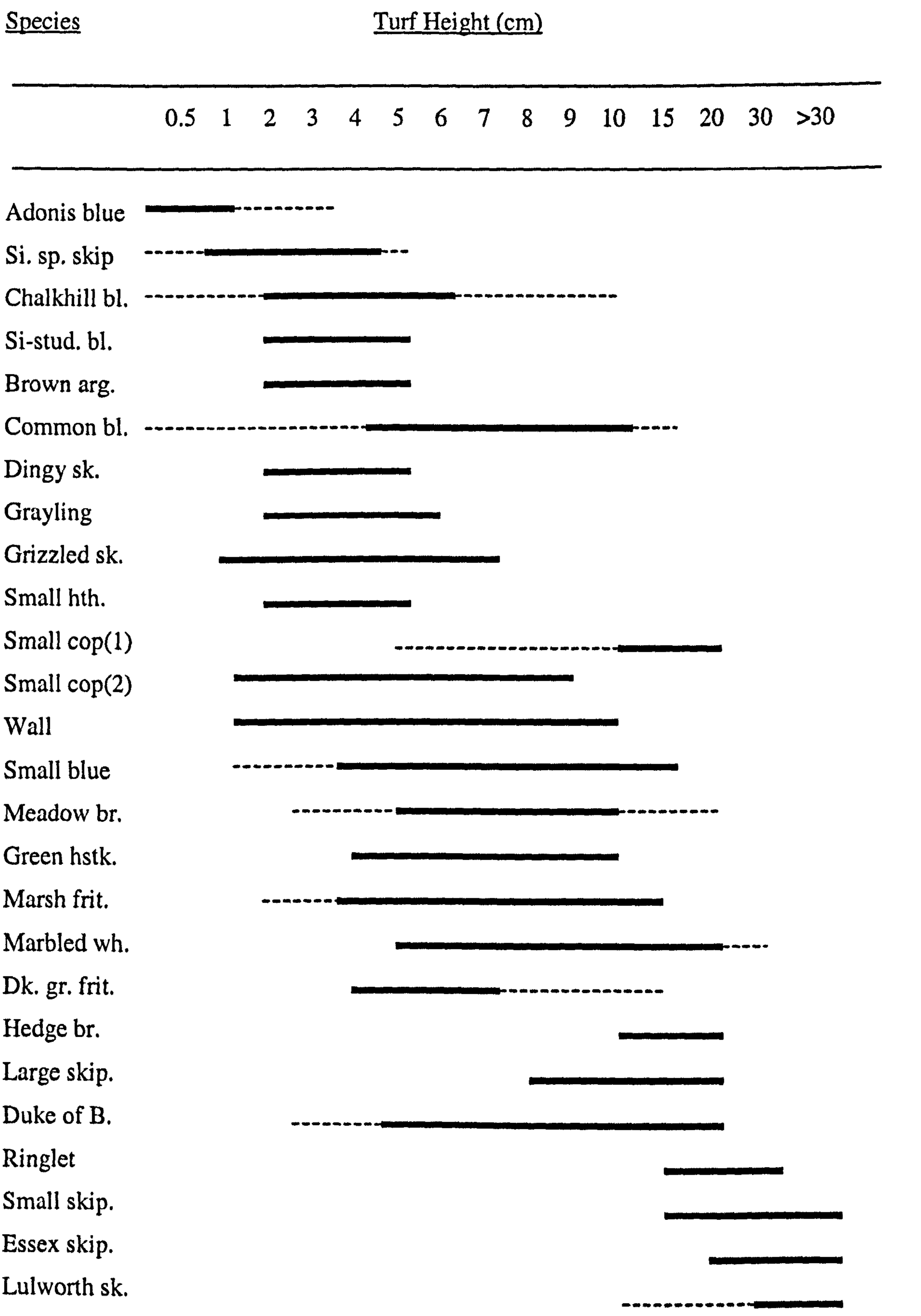
structural elements. Warren's (1995) description of high brown fritillary *Argynnis adippe* habitat selection is one of only a few to do so.

Porter *et al* (1992) described partitioning by habitat in closely related butterflies and extended the concept by drawing on descriptive work for chalk grassland butterfly "preferred turf height" given in the Butterflies Under Threat Team report (BUTT 1986). This neatly showed that very few species occupying this habitat have a shared mid-range of preferred turf (sward) height, despite using different ranges of larval food-plants and nectar sources and therefore possessing low niche overlap values for these. The preferred turf heights are reproduced in Figure 1.1.

Porter *et al* (1992) also described relationships between butterflies and plants that impinge on habitat partitioning and species' habitat selection such as chemical defences (against larval 'predation'), physical defences (such as thick cuticles and spines), pollination mechanisms and butterfly-host plant coevolution.

It was J. Thomas (1993) who first pointed out that many British species occupy early successional stages of vegetation. He showed that ten species, including chalk grassland specialists such as adonis blue *Lysandra bellargus* and silver-spotted skipper *Hesperia comma*, occupied very narrow and ephemeral niches, breeding near the ground in the earliest habitat seral stages. He suggested that these species were relicts from previous climatically warmer eras and would have become extinct if man had not produced the widespread early seral stage habitats.

Figure 1.1: Preferred turf heights for British grassland butterflies. (From BUTT 1986).



C. Thomas (1995) pointed out that many British butterflies breed in successional or plagioclimactic vegetation. Good examples are three woodland fritillaries, the heath *Mellicta athalia*, small pearl-bordered *Boloria selene* and pearl-bordered fritillary *Boloria euphrosyne*, all of whom occupy woodland habitats for the first few years of succession after canopy clearance (Warren and Thomas 1992). The silver-studded blue *Plebejus argus*, is known to occupy relatively short stages (5-10 years) of early succession on heathland (Thomas and Harrison 1992). Grasslands are often a complicated mosaic of successional patches and semi-natural chalk grasslands are a good example of this, with short turf on thin skeletal soils on slopes, taller turf, usually consisting of different vegetation communities on deeper loams (Rodwell 1992), together with scrub and track edges. Erhardt (1985) showed that early successional stages of abandoned sub-alpine meadow grasslands in Switzerland had the highest butterfly diversity. Similar studies in woodland have shown a high degree of correlation between butterfly diversity and physical and vegetation species components (Porter *et al* 1992 using data from Peachey 1980). This butterfly-plant diversity correlation is mirrored at the species level where some species require a number of different host-plants in different seasons, such as holly blue *Celastrina argiolus*, or even at different stages of larval development such as marbled white *Melanargia galathea* (BUTT 1986).

Thomas and Jones (1993) showed how habitat heterogeneity was important to silver-spotted skipper survival, where, in drought years, the butterfly was able to utilize more sheltered areas with longer swards to enable the population to persist. This need for resource heterogeneity was also shown by Carey (1994) who showed that egg densities of the silvery blue butterfly *Glaucopsyche lygdamus* in Colorado were correlated only with measures of total host-plant diversity and not with any single host-plant species. This

butterfly's larval host-plants were all ephemeral and in young growth stages and therefore extremely vulnerable to drought and late frosts. An adaptation to wider host-plant niches is clearly necessary for population persistence in poor years for any one, or groups of, host-plant species. Habitat heterogeneity has been shown to (negatively) correlate strongly with population variability in other insect groups such as Orthoptera (Kindvall 1996).

Much of the modern debate and theory on metapopulation dynamics has assumed that patch networks consist of individual patches, which vary in size and inter-patch distance but not necessarily quality of habitat. Hanski (1999 after Gyllenberg and Hanski 1997) discusses patch quality as an adjunct to the rescue effect (Section 1.5) as a factor which is likely to affect the relationship between the fraction of empty patches and the amount of suitable habitat. He showed that as habitat destruction is associated with a decrease in remaining habitat quality, the fraction of empty patches at equilibrium should also increase. The quality of the empty patches becomes even more important for metapopulation growth (Nee 1994). However, intra-patch habitat quality is a very difficult variable to build into the metapopulation models and despite formulating habitat quality effects on isolation and long-term probability of patch occupancy (Moilanen and Hanski 1998), it has been excluded from the core Incidence Function Model (Moilanen pers. comm.).

1.5 HABITAT FRAGMENTATION

Habitat fragmentation is distinct from habitat loss in that the former is defined as the remaining habitat of fixed total area is located in increasingly smaller and more isolated discrete patches or fragments (Hanski 1999) between which habitat loss is occurring.

Habitat fragmentation affects the connectivity between patches, which is a major area of investigation in metapopulation studies, but there is also an increase in relative amount of habitat edge which may become a major factor to local populations (Harris 1988; Mills 1995).

Habitat fragmentation is a fundamental property of metapopulation ecology and is intimately linked with the effect of patch isolation on colonization (Hanski 1999).

Hanski (1999) suggests that in the early stages of habitat destruction, while remaining habitat is still well connected, populations are primarily affected by habitat loss. At this time, population sizes are related to the total area of remaining habitat. As habitat destruction continues, connectivity between remaining patches is reduced, compounding the effect of habitat loss, until at around 50 per cent loss, the total effect suddenly increases exponentially (Bascompte and Sole 1996). In practice, the effect appears to be delayed until the proportion of habitat loss is higher due to migration across unsuitable habitat and non-equal spatial loss of habitat (Andren 1994).

Levins (1969 and 1970) was the first to provide a realistic metapopulation model which showed that metapopulation persistence is a stochastic balance between local extinctions and recolonizations of empty habitat patches. The model is described by:

$$\frac{dP}{dt} = cP(1 - P) - eP$$

where $P(t)$ is the fraction of patches occupied at time t, and c and e are colonization and extinction rates respectively.

The model does however describe a deterministic rate of change (although based on stochastic local extinctions), assumes an infinite number of habitat patches and that colonization is not affected by distance. Modification of the original model by parameterization of the habitat loss (May 1991; Nee and May 1992; Lawton *et al* 1994 and Nee 1994), has led to the realisation that a simplified rule, the 'Levins rule' (Hanski 1996) can be applied. This states that "A sufficient condition for metapopulation survival is that the remaining number of habitat patches following a reduction in patch number exceeds the number of empty but suitable patches prior to patch destruction". However, applicability of this rule appears mixed for a number of reasons, one of which is the very important rescue effect (Brown and Kodric-Brown 1977), which, in metapopulations with a mainland-island structure, is simply the effect of constant migration from the mainland to the islands which reduces the risk of extinction termed a 'pseudo-rescue' effect by Hanski (1999). In non mainland-island situations, however, the effect is more diffuse, with local interactions varying according to local population sizes, patch size and inter-patch distances.

1.6 PATCH AREA

Patch area is the second fundamental property of metapopulation ecology (together with patch isolation) and is intimately linked with extinction rates (Hanski 1999). Patch area and isolation have been termed the first-order landscape effects on population biology (Hanski 1999).

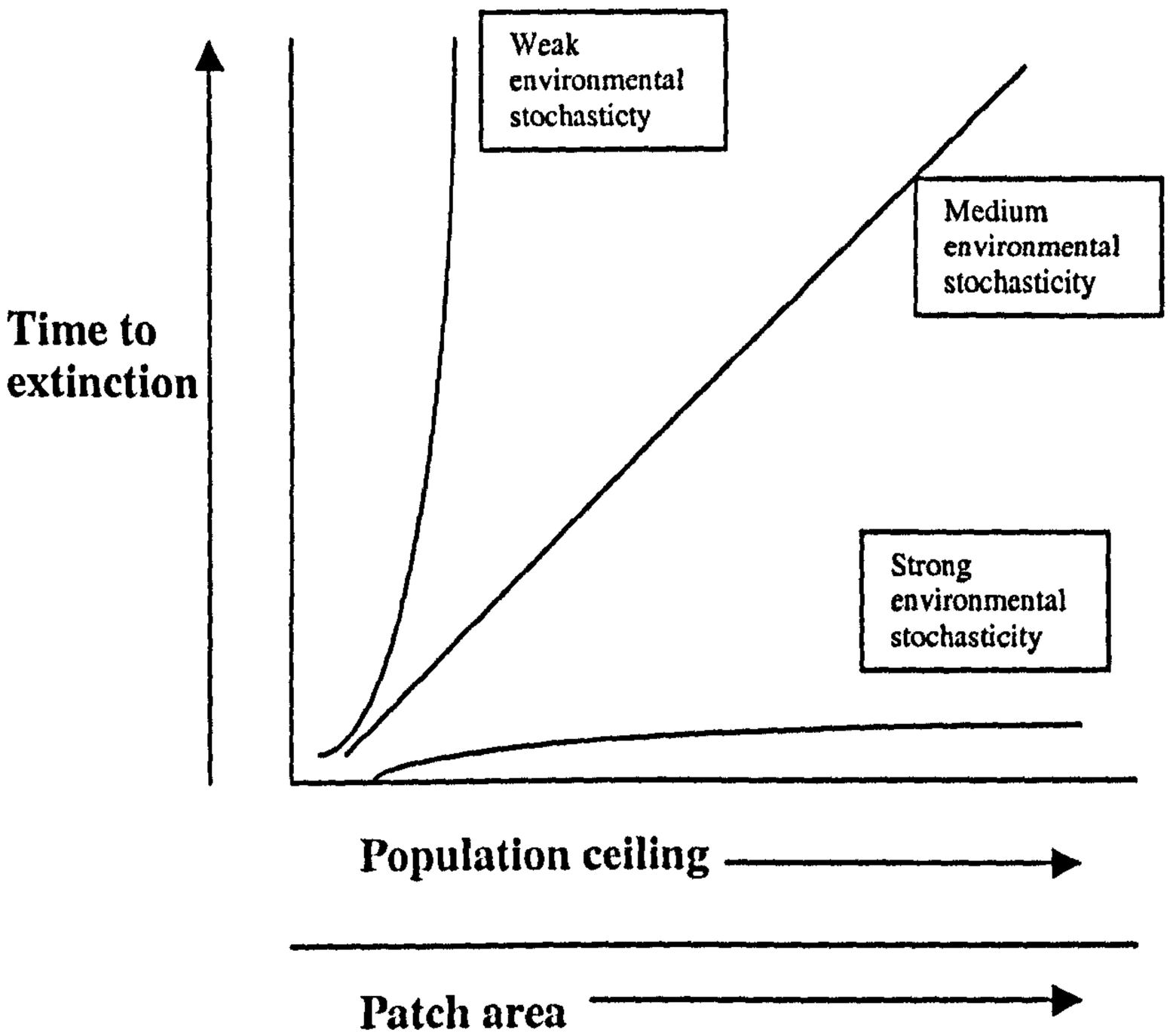
The relationship between patch area and time to extinction for a local population becomes steeper (greater time to extinction for a smaller patch area), where populations are exposed

to weaker environmental stochasticity. There are various possible reasons for this relationship. One is that as patches get larger, the carrying capacity (k) of the population increases and the effect of environmental stochasticity is reduced. In addition, larger patches also exhibit a greater variety of habitats which hold important secondary resources when environmental conditions produce stress on primary resources (Ehrlich and Murphy 1987). The relationship is summarized in Figure 1.2 (adapted from Figure 2.5a in Hanski 1999). These two effects may have different influences on small (carrying capacity) and large (habitat heterogeneity) populations. Indeed, the species-area curve which is such a widespread phenomenon in community ecology (MacArthur and Wilson 1967), may actually be a 'reverse function' of the extinction-area effect (Hanski 1999).

These relationships are fundamental to the role of habitat patches as 'source and sink' habitats. These terms relate to those patches which contain populations which contain source (where intrinsic rate of increase $r > 0$) or sink (intrinsic rate of increase $r < 0$) populations and are therefore net contributors to or users of metapopulations. In some circumstances, populations exist where deaths exceed births at equilibrium and decline to a new equilibrium level rather than extinction due to the presence of other populations. Habitat patches containing such populations have been termed 'pseudo-sinks' Watkinson and Sutherland 1995).

A classic British example of a species existing in source-sink metapopulations is the marsh fritillary *Eurodryas aurinia*. Metapopulations have consisted of a number of persistent local populations interspersed with highly variable local populations in apparently poor quality habitat (Warren 1994). Many of the latter go extinct for short periods, obviously re-colonizing from the persistent (source) populations in good years.

Figure 1.2: Relationship between time to metapopulation extinction and population ceiling or patch area.



1.7 POPULATIONS AND METAPOPULATIONS IN A LANDSCAPE CONTEXT

The theoretical approach to populations and metapopulations discussed in the previous sections views local population dynamics as being density-dependant within patches and more or less asynchronous between patches. If migration rates between patches are relatively large in relation to inter-patch distance, then local patch population dynamics can begin to mix together and behave as a single large local population.

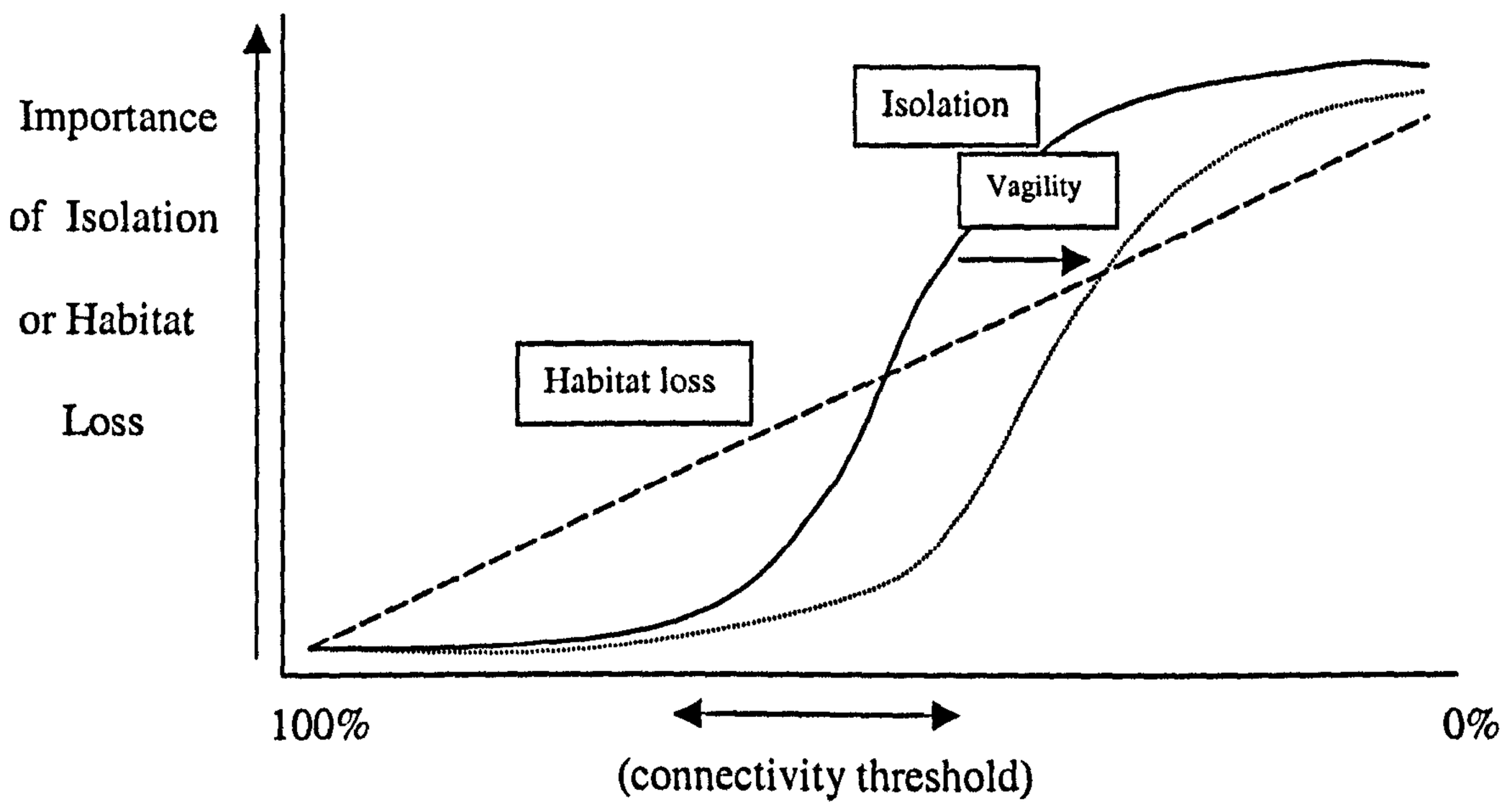
Wiens (1997) gave a resume from a landscape ecology point of view, pointing out that patch occupancy, size and shape all vary and that making spatially explicit metapopulation models is a necessary process but is not sufficient to fully describe dynamics in a landscape context. He further demonstrated that the more realistic model is a complex mosaic of inter-patch habitats which include corridors and boundaries and that therefore inter-patch distances are not Euclidian but a complex function of boundary permeabilities and relative patch 'viscosities' to a migrating organism. He added that other aspects of metapopulation structure, including dynamics of the patches themselves (and therefore patch extinction probability), must be influenced by landscape structure.

Much of the empirical evidence to support Wiens' view comes from the non-linear effects of scale on populations at a landscape scale. For example, if continuous habitat is fragmented, initial effects are due to the loss of habitat alone. As loss continues, a threshold is reached where the effect of patch isolation becomes more important and increasing fragmentation accelerates the inter-patch distances and therefore isolation. This has been shown to be the case for both birds and mammals (Andren 1994) and is summarized in Figure 1.3.

From a landscape ecologist's point of view, the recent emphasis on spatially explicit metapopulation modelling need a shift of scale from movements and patches defined by individual home ranges to broader scale movements of populations combined with a scale of patchiness modelled from interactions within a local population. One of the best examples of the over-simplification of 'landscape' measurement is probably the classic species-area curve in Island Biogeography Theory (MacArthur and Wilson 1967). The scatter of points above the line have been interpreted as 'supersaturation' of species while

those below the line have been interpreted as the result of disturbance and extreme isolation. The scatter is much more likely to be at least partly a combined effect of connectivity, patch context and edge conditions (Wiens 1989).

Figure 1.3: The hypothetical relationship between the proportion of suitable habitat in a landscape and the relative importance of habitat loss and patch isolation to individual movement or population dynamics. Vagility is a measure of mobility across the landscape elements and effects the position of the connectivity threshold. (From Wiens 1997).



1.8 AIMS OF THE RESEARCH

The overall aim of the current research project is to investigate the relative importance of landscape and habitat for chalk grassland butterflies both at the 'local' scale (i.e. within habitat blocks), and at the landscape scale (i.e. among habitat patches).

This is to be done by the following steps:

1. Species analysis

   a) Describe species' habitat selection and resource needs within a single, contiguous large chalk grassland site where landscape scale processes are assumed to be minimised;

   b) Carry forward the local scale models from above to incorporate in a landscape scale analysis of fragmented patches of chalk grassland in an agricultural/forested landscape;

   c) Additionally use the local scale models in an intermediate scale analysis among less well defined habitat patches within the single, contiguous large patch of chalk grassland.

   Use independent sites (or sub-sites), to test between-site and between-year predictive power of models constructed in each of the three analyses above.

2. Community analysis

   To determine species' relationships as described by their positions along environmental gradients which may be combinations of habitat, environmental or landscape factors.

3. For a selected number of species, to model parameters relating to metapopulation processes.

4. To relate results from each of these processes to current knowledge of chalk grassland butterfly population ecology and to investigate whether methods and results can be used to aid a simplified approach to the study of butterfly population processes and to aid nature conservation planning at the local and landscape scales.

Small heath

Picture: Simon Coombes

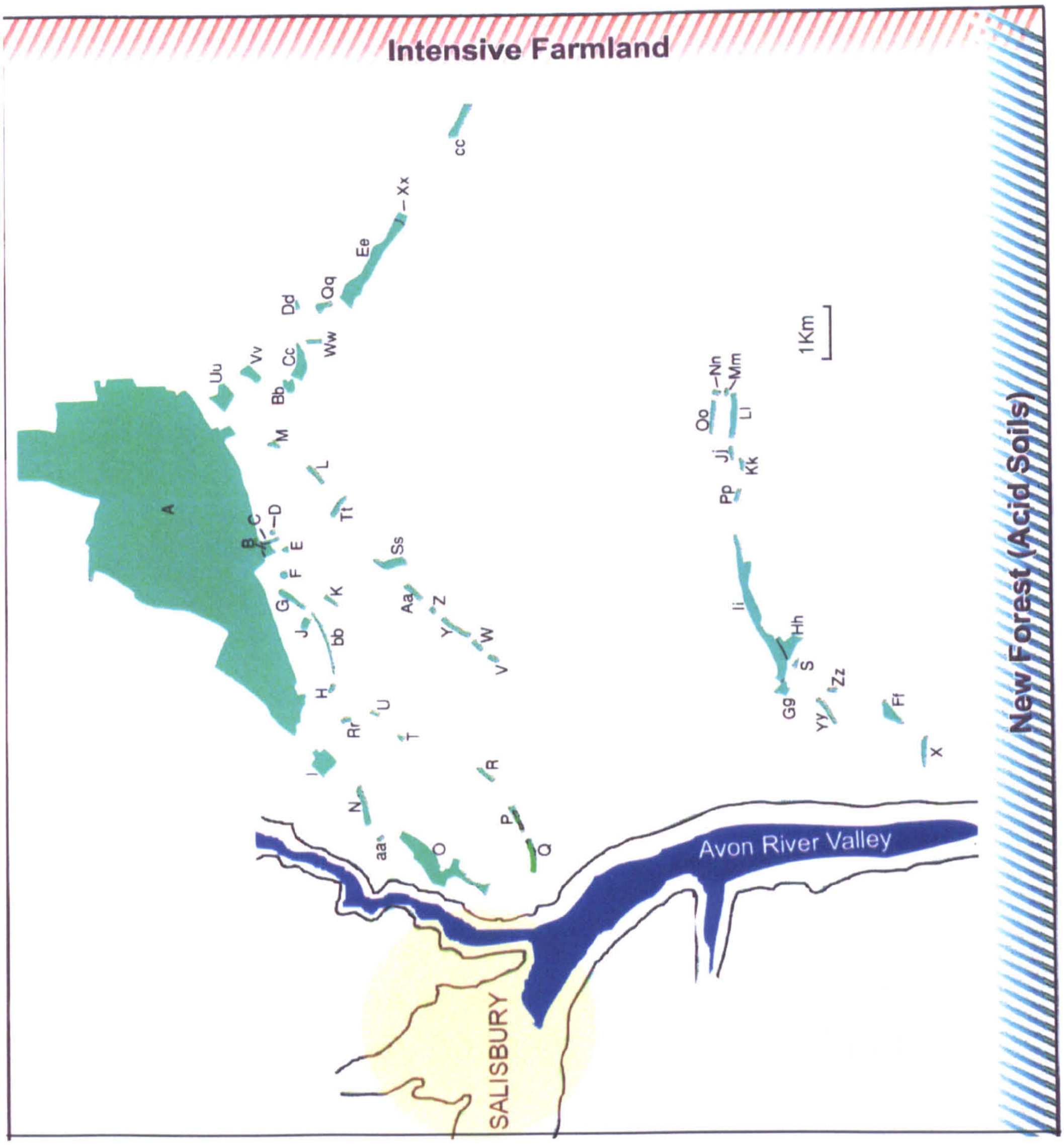
2. METHODS

2.1 STUDY AREA

The study area encompassed a series of calcareous grassland patches south of Salisbury Plain on the Wiltshire/Hampshire border in southern England. The sites were located in an area of approximately 160 km^2 bounded by Porton Down to the north, the broad valley of the River Avon to the west, the acid soils and heaths of the New Forest to the south and intensive farmland to the east. The relative location of Porton Down and the other sites, referred to as the Fragmented Sites in this study, are shown in Figure 2.1. The full list of site names, Ordnance Survey grid location patch area and codes to locations in Figure 2.1 are shown in Table 2.1.

A single, large patch of calcareous grassland formed the northern boundary of the suite of study sites. This site, Porton Down, is owned by the Defence Evaluation and Research Agency (DERA), an agency of the Ministry of Defence (MoD), and has been used for chemical weapons and defence experimentation since the Government acquired the area in 1918. The DERA estate at Porton Down totals 2773 ha of which approximately 1700 ha is calcareous and mesotrophic grassland. The highest quality grassland makes up the majority of 1227 ha which have been designated Site of Special Scientific Interest (SSSI), Special Protection Area (SPA) and proposed Special Area of Conservation (pSAC), the latter together with Salisbury Plain and Parsonage Down. The DERA/MoD describe Porton Down as their "jewel in the crown" as it is rich in biodiversity.

Figure 2.1: Map showing location of Porton Down and Fragmented Sites relative to major regional features.



It is the second largest remaining tract of calcareous grassland in Britain, has 46 recorded species of butterfly (the highest of any site in Britain), regularly hosts 12 per cent of the UK's breeding stone curlew *Burhinus oedicnemus* population, holds sixteen species of orchid and over 700 species of macrofungi and is home to some three million yellow meadow ant *Lasius flavus* nests containing some 35 billion ants (Porton Down

Dark green fritillary

Picture: Simon Coombes

Ant-hill communities at Porton Down

Conservation Group Site Dossier). In addition, the area has an extremely important suite of Neolithic and Bronze Age archaeological remains. Although much of the site has been

shallow ploughed in the last few centuries (Wells *et al* 1976), the lack of modern agricultural disturbance and the recolonisation potential of the core, undisturbed areas, has ensured the conservation of this unique ecological resource.

Partly in recognition of the site's ecological importance, Porton Down became the UK's tenth terrestrial Environmental Change Network (ECN) site in 1994. The ECN is the UK's foremost integrated environmental monitoring network sponsored by participating organisations and co-ordinated by CEH Merlewood (Sykes and Lane 1996). This study draws on some of the data collected for the ECN by the author who was ECN Site Manager during the period February 1994 to February 2000.

The Fragmented Sites were located from previous work or by searching the area (see Section 2.3.2). 'Quality' and type of calcareous grassland within each site was very varied and ranged from highly managed SSSIs such as Broughton Down to the many rank, ungrazed smaller patches in the network. Permission for access to these sites was obtained during the winter of 1995-1996.

<u>Battery Hill (Porton Down) and surrounding farmland</u>

Table 2.1: Site names, Ordnance Survey grid location, patch area and map code

Name	Central OS grid reference	Area	Map Code
Porton Down	SU24003640	1942.00	A
Pheasant Field:			
NW Corner	SU22903495	1.28	B
Long Strip	SU23053500	0.15	C
Double Tumulus	SU23133495	0.25	D
Field @ Gate 13	SU22923472	0.32	E
S of Winterslow. Firs	SU22443475	0.75	F
Winterslow Firs	SU21983458	4.60	G
Area @ Gate 14/15	SU20323369	0.30	H
Figsbury Ring	SU18883385	12.30	I
Thorney Down Tip	SU21323437	1.50	J
Jowett's Clump	SU22053390	0.69	K
Gutteridge's Farm	SU24463438	2.15	L
Lopcombe Corner	SU25003503	0.30	M
Bracknell Croft SSSI	SU18103308	3.50	N
Cockey/Laverstock			
Downs (part) SSSI	SU16853150	27.00	O
King Manor Hill:			
Palace/Picnic Area	SU17903005	0.60	P

Table 2.1: (Continued)

Partridge Bank	SU17222967	2.50	Q
Savage's Farm	SU18653068	1.20	R
Witherington Down East	SU21022471	0.20	S
Fussell's Lodge Road	SU19303230	0.30	T
Stock's Bottom	SU19781993	0.60	U
Pitton Downs:			
White Hill S	SU20943067	1.00	V
White Hill N	SU21183096	1.35	W
Barford Lane	SU19182203	3.00	X
Pitton Downs:			
a	SU21553153	1.20	Y
b	SU21923191	1.20	Z
c	SU22163214	2.15	Aa
Ashley's Copse	SU26183474	4.70	Bb
Bussle's Wood	SU26683451	5.40	Cc
Kestrel's Farm	SU27443456	0.40	Dd
Broughton Down SSSI	SU28503330	42.70	Ee
Barford Down	SU20072282	11.25	Ff
Witherington Down West	SU20552493	6.70	Gg
Pepperbox Hill SSSI	SU21352480	7.00	Hh
Brickworth Down SSSI	SU22002555	32.50	Ii
Whitehouse Copse Ride	SU24972600	0.63	Jj

Table 2.1: (Continued)

Whitehouse Copse East	SU24862584	2.00	Kk
Royal Naval Armaments			
Depot (RNAD):			
South Section	SU26102645	7.26	Ll
Woodland Glade	SU26032723	0.23	Mm
Juniper Area	SU25552733	1.60	Nn
North Banks	SU25752647	5.00	Oo
Whitehouse Copse West	SU24322589	0.80	Pp
Bullock's Hole	SU27713421	4.25	Qq
Stockbottom Farm	SU19583340	0.12	Rr
East Winterslow	SU22483279	4.34	Ss
E Winterslow Droveway	SU24003388	0.25	Tt
Little Firs farm	SU25553582	3.92	Uu
The Anchorage	SU26003547	4.13	Vv
Bussle's Wood Droveway	SU27093443	0.19	Ww
Broughton Down SSSI			
Extension	SU29473267	2.80	Xx
Standlynch Droveway	SU20352422	0.21	Yy
Witherington Dn. Reservoir	SU20662417	0.06	Zz
Cockey Bottom	SU17213261	0.12	aa
Thorney Down Bank	SU21243400	0.91	bb
Bossington	SU32133120	4.69	cc

2.2 BUTTERFLY SURVEY

2.2.1. Selection of species to be studied

Species names and taxonomic affiliations follow Thomas and Lewington (1991).

The first criterion for selection of species to be studied was that only species which were non-migrant and non-irruptive should be included. Inclusion of these species would have masked habitat selection analyses. This effectively excluded three of the whites (Pieridae: large white *Pieris brassicae*, small white *P.rapae* and green-veined white *P.napi*) and four of the nymphalids (red admiral *Vanessa atalanta*, painted lady *Cynthia cardui*, small tortoiseshell *Aglais urticae* and peacock *Inachis io*).

The selection of which other species should be incorporated in the study was largely guided by criteria incorporated in management documents and by knowledge of regional butterfly habitat selection behaviour. For example, the twenty-seven species selected for discussion in the Butterflies Under Threat Team document (BUTT 1986), included two (Lulworth skipper *Thymelicus acteon* and silver-studded blue *Plebejus argus*) which did not occur in the Porton Down study area. Two other species, brimstone *Gonepteryx rhamni* and holly blue *Celastrina argiolus*, were felt to be too wide-ranging in terms of within-season mobility and habitat requirements (see Pollard & Yates 1993) to be assignable as 'chalk grassland' species in this study. This left 23 species for inclusion in the study (Table 2.2).

Table 2.2: Species included in the study

Taxonomic Group	Common name	Scientific name
Hesperidae	small skipper	*Thymelicus sylvestris*
	Essex skipper	*Thymelicus lineola*
	silver-spotted skipper	*Hesperia comma*
	large skipper	*Ochlodes venata*
	dingy skipper	*Erynnis tages*
	grizzled skipper	*Pyrgus malvae*
Lycaenidae	green hairstreak	*Callophrys rubi*
	small copper	*Lycaena phlaeas*
	small blue	*Cupido minimus*
	brown argus	*Aricia agestis*
	common blue	*Polyommatus icarus*
	chalkhill blue	*Lysandra coridon*
	adonis blue	*Lysandra bellargus*
Riodinidae	Duke of Burgundy	*Hamaeris lucina*
Nymphalidae	dark green fritillary	*Argynnis arglaja*
	marsh fritillary	*Euphydryas aurinia*
Satyridae	wall	*Lasiommata megera*
	marbled white	*Melanargia galathea*
	grayling	*Hipparchia semele*
	hedge brown	*Pyronia tithonus*

Table 2.2 (Continued)

	meadow brown	*Maniola jurtina*
	ringlet	*Aphantopus hyperantus*
	small heath	*Coenonympha pamphilus*

2.2.2. Selection of Butterfly Sampling Method

As the proposed study was intended to be wide-ranging in terms of species and geography it was decided that presence-absence data would be an acceptable measure, together with indices of relative abundance where appropriate. The alternative measure to an index for each species would have been an absolute population measure. This would have required a large amount of marking and re-capturing work which would have probably enabled only a few species to be studied due to the time and labour resources required.

An adaptation of the method which gives the Index of Abundance measure used by the British Butterfly Monitoring Scheme (BMS - Pollard and Yates 1993) appeared to be the most appropriate for the present study. This method requires weekly species counts along transects. These counts are then summed to give a population index. The rationale behind this measure is that adults of most British butterflies have individual life spans of approximately seven days and therefore weekly counts will give an approximate area under the population curve, as in approximation methods in integral calculus. Populations are uniformly sampled by recording butterflies in a moving 5x5 metre area in front of the slowly walking observer. Statistical checks on the relationship between the BMS Index

Brown argus

Picture: Simon Coombes

Marbled white

Picture: Simon Coombes

Silver-spotted skipper

Picture: Simon Coombes

and populations calculated from mark-recapture studies have been performed by other workers (see e.g. Zonneveld 1991) and appear to be consistent among univoltine species.

Two BMS transects were set up at Porton Down, the first under the ECN Programme from 1994, the second an additional voluntary one carried out by Mr R. Ryan from 1995. Data from these transects were used for comparative purposes and in statistical analysis of research transect data (see Section 2.6.1).

This study has required an adapted Index of Abundance measure, since individual (sub-) populations could not be sampled weekly. This is explained in Section 2.5 'Statistical Analysis'.

The sex of the Blues (Lycaenidae) was also recorded as were any additional species seen outside the recording box and in the same habitat patch.

Individual populations were mostly sampled using 200 metre long transects stratified within vegetation types (see Section 2.3). This is approximately the average length of transects used to sectionalise BMS monitoring sites. At Fragmented Sites, 200 metre transects could not always be fitted in to sample habitats. Data from these shorter transects were standardised accordingly (see Section 2.5 'Statistical Analysis').

Other criteria used for the BMS were also adopted for this study. These are:

* Time of recording to be restricted to between the hours of 10:45 and 15:45 BST.

* Ambient temperature should be >13 degrees Celsius if 60 per cent or more sun, while if the temperature is >17 degrees Celsius, the amount of sunshine is not relevant.

* Surveys should not take place if it is raining or wind is greater than Force 5 on the Beaufort Scale ($\cong 9\ m^{-s}$).

In marginal weather conditions, these criteria were slightly adapted to be applied as averages for groups of transects if field work had already started on them. Also, the time period was allowed to be flexible on very fine days in mid-summer.

2.2.3. Butterfly Recording Period

The butterfly recording period for all survey years was 1 May to 30 September. This period encompassed the average first emergence date for spring emerging species and most of the flight period for all but the last few individuals of late summer univoltine species (such as meadow brown *Maniola jurtina*) and second broods of bivoltine species (such as common blue *Polyommatus icarus*, adonis blue *Lysandra bellargus* and brown argus *Aricia agestis*). Small copper (*Lycaena phlaeas*) presented a problem in that it often has a third brood in good summers, which is on the wing well into October in some years. However, it was not felt feasible to carry on survey work to add data for one species.

Battery Hill (Porton Down) showing ranker mesotrophic grassland growing on deeper soil in the foreground with rabbit-grazed calcareous grassland in the background

Species-rich CG2 grassland at Porton Down with much evidence of rabbits and a silver-spotted skipper nectaring on self-heal *Prunella vulgaris*

Transects on Porton Down were visited according to which areas of the working Range were accessible. The order of first visits generally dictated the order of subsequent visits, again, depending on access. As soon as one round of visits finished, the next round started independent of date. In this way, it was hoped that there would be a visit to each transect at least once during the flight period of every butterfly species to be surveyed.

Transects on Fragmented Sites were visited under similar criteria as those above, with access permission being the most restricting factors. Again, the order of initial visits largely dictated the order of subsequent visits.

2.3 SELECTION OF SAMPLING AREAS

2.3.1 Porton Down

It was known from previous surveys (Wells *et al* 1976; Wilson and Reed 1992) that the semi-natural chalk grassland on the Porton Ranges fell into five major categories of classification according to the National Vegetation Classification, ('NVC' – Rodwell 1992). These are shown in Table 2.3.

There were also small areas of 'Acid Heath' often with heather *Calluna vulgaris* and also tor-grass *Brachypodium pinnatum* dominated areas, akin to the CG4 NVC type. Additionally, small areas of more mesotrophic grassland which could be classified as crested dog's-tail-black knapweed *Cynosurus cristatus - Centaurea nigra* (MG5) and rye grass-crested dog's-tail *Lolium perenne - Cynosurus cristatus* (MG6 NVC type). Where

either of these latter two NVC types occurred on samples, they were assigned to a single 'MG5/6' group.

Table 2.3: NVC categories found on Porton Down.

MG1 – False oat-grass *Arrhenatherum elatius* grassland

CG2 – Sheep's fescue-meadow oat-grass *Festuca ovina-Avenula pratensis* grassland

CG3 – Upright brome *Bromus erectus* grassland

CG6 – Hairy oat-grass *Avenula pubescens* grassland

CG7 – Sheep's fescue-mouse-ear hawkweed-thyme *Festuca ovina-Hieracium pilosella-Thymus spp* grassland

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In addition, vegetation monitoring under the ECN Project, had identified two scrub communities on Porton Down which could be ascribed to the W21 hawthorn-ivy *Crataegus monogyna-Hedera helix* scrub and W24 blackberry-Yorkshire fog *Rubus fruticosus-Holcus lanatus* underscrub NVC types. These were not typically present in historically open grassland areas, but in woodland clearings, particularly where storm damage had occurred and at grassland 'break' areas. Other scrub was usually ascribable to 'scrubby' open grassland types (grassland NVCs with scrub species as associates).

These NVC types had been mapped by Wilson and Reed in 1991, and it was felt reasonable to assume that these maps would still be relevant to grassland communities on the ground in 1995. These areas therefore formed the basis of a stratified sampling system

for butterfly populations. Copies of the vegetation maps from Wilson and Reed (1992) are shown in Appendix 1a-d.

2.3.2 Fragmented Sites

A total of 42 sites, with the range 0.07 ha to 42.7 ha were initially identified as potential butterfly survey sites from maps, aerial photographs and previous surveys.

Many of these sites had been surveyed by English Nature during a wider survey of remnant chalk grassland in Wiltshire during the period 1989-1990 (McSweeney 1991). Some information required for stratification of samples could be gleaned from NVC maps resulting from this work. For sites without this information, pre-sampling visits were made during February and March 1996 in order to assess approximate NVC types and area.

A further 12 sites were subsequently found and surveyed in 1997. Data from these sites were used to test statistical models from the 1996 sites but were added to the sites surveyed in 1996 for an Incident Function Model analysis (see Section 2.7).

2.3.3 Placement of Transects

This was initially a map-based exercise using mapped NVC areas as described in 2.3.1 and 2.3.2 above.

For Porton Down, an initial set of 100 200m long transects were drawn on a vegetation map, ensuring that each transect covered no more than one mapped NVC type. If grassland NVC areas were large enough to contain more than one transect, they were placed either end-to-end or a minimum of 200m apart laterally. If the grassland NVC area was less than 200m wide, then no transect was placed within it. Subsequently, transects were either moved or added to, in order that areas were sufficiently sampled by stratified area and NVC type, with a rule that no two transects were nearer than 100m apart laterally. Numbers of transects were apportioned according to known total areas of NVC, once the mapping exercise was completed. NVC types and numbers of transects are shown in Table 2.4. Transect locations are shown in Figure 2.2.

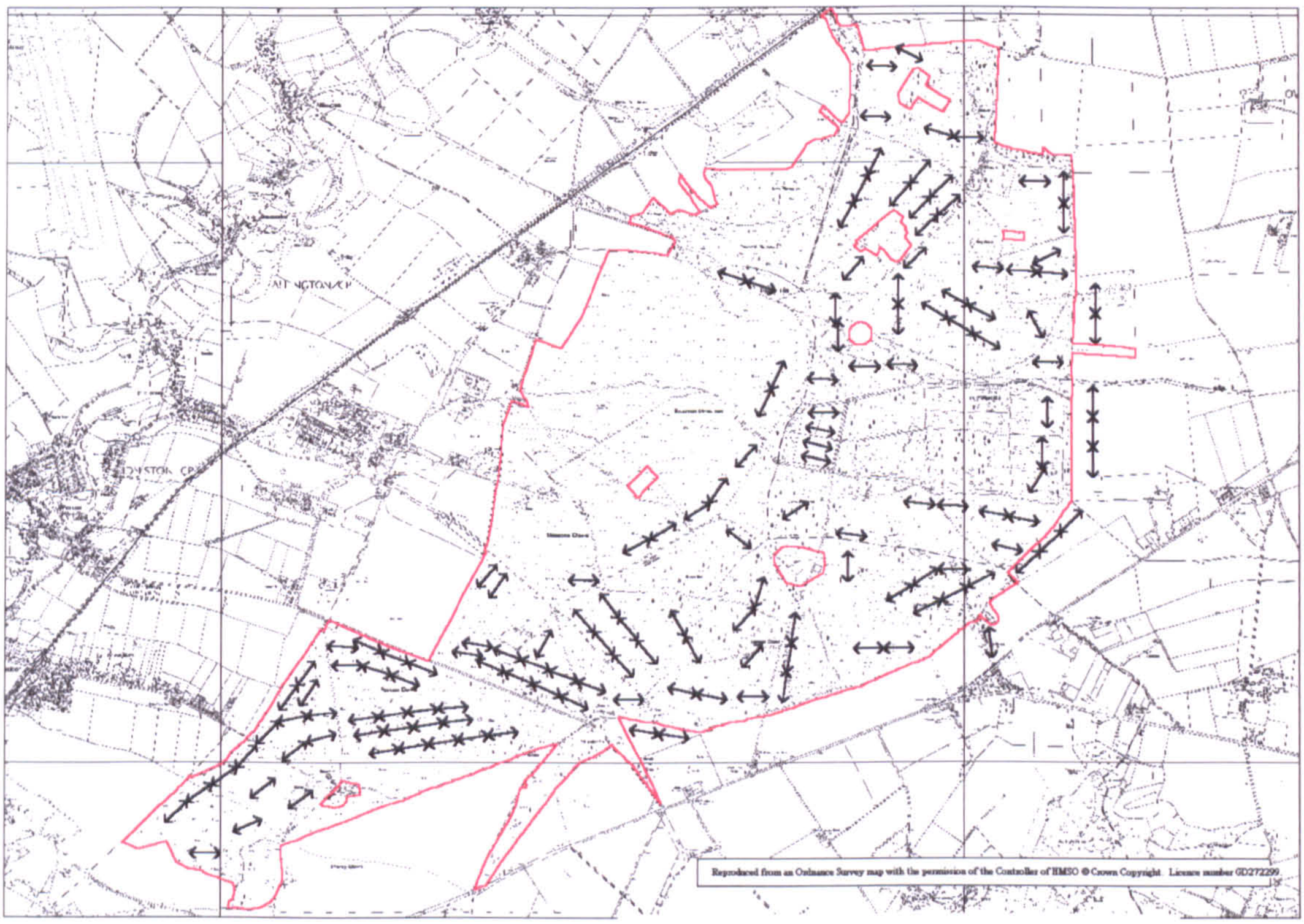
For Fragmented Sites, a total of 99 transects (originally 100 but one was 'lost'), were placed on maps in the same stratified manner as on Porton Down, except where small sites had more than one (or a mosaic) of NVC types. In this case, single transects were positioned such that transect length was maximised across all grassland NVC types. Numbers of transects per site ranged from one to 10. Sites and transect data are given in Appendix 2. NVC types identified from the McSweeney survey and represented on transects in the 1996 survey are shown in Table 2.5. These figures are frequencies as many transects covered more than one NVC type.

Table 2.4: Number of transects per NVC type at Porton Down

NVC	No. Transects
MG1 - False oat-grass *Arrhenatherum elatius* grassland	11
CG2 - Sheep's fescue-meadow oat-grass *Festuca ovina-Avenula pratensis* grassland	16
CG3 – Upright brome *Bromus erectus* grassland	24
CG6 – Hairy oat-grass *Avenula pubescens* grassland	13
CG7 - Sheep's fescue-mouse-ear hawkweed-thyme *Festuca ovina-Hieracium pilosella-Thymus spp* grassland	51
Unclassifiable - mainly common rock-rose *Helianthemum chamaecistus* 'Antscape' vegetation	10
Further transects which were placed in unclassified vegetation	27
Total	152

The remaining transects were not classified previous to the botanical assessment in this study.

Figure 2.2: Locations of butterfly research transects on Porton Down. Each 200m section is denoted by arrows. Boundary of SSSI/SPA/pSAC shown by red line



Green hairstreak

Picture: Simon Coombes

Table 2.5: NVC types represented on transects on Fragmented Sites surveyed in 1996

NVC	Frequency on Transects
MG1 - False oat-grass *Arrhenatherum elatius* grassland	12
MG5/6 - Semi-improved mesotrophic grassland	13
CG2 - Sheep's fescue-meadow oat-grass *Festuca ovina-Avenula pratensis* grassland	34
CG3 - Upright brome *Bromus erectus* grassland	14
CG6 - Hairy oat-grass *Avenula pubescens* grassland	0
CG7 - Sheep's fescue-mouse-ear hawkweed-thyme *Festuca ovina-Hieracium pilosella-Thymus spp* grassland	1
W21 - Hawthorn-ivy *Crataegus monogyna-Hedera helix* scrub and W24 blackberry-Yorkshire fog *Rubus fruticosus-Holcus lanatus* underscrub	0

For the Fragmented Sites covered in the 1997 survey, there was no prior knowledge of NVC communities.

2.4 HABITAT AND ENVIRONMENTAL VARIABLES

2.4.1 Recording Methods

In 1995, 60 sample transects were randomly selected from the Porton Down set, stratified across grassland NVC types to provide a representative sample. At each transect, between 5 and 10 points were selected using random numbers between 0 and 200. At each of these points, the following variables were recorded in a 1x1m square quadrat (unless otherwise stated):

1. Location (metres from the start of the transect).
2. Slope (degrees from horizontal across the quadrat location).
3. Aspect (on a sixteen point scale i.e. North, North-north East, North-east, etc).
4. a. Number of rabbit fecal pellets < 8 days old.

   b. Total number of rabbit fecal pellets.

   c. Number of rabbit fecal pellets < 8 days old in an expanded 2x2m area.

   d. Total number of rabbit fecal pellets in the expanded 2x2m area.
5. Sward height in centimetres at five points, 1m apart along a perpendicular line, centred on the quadrat.
6. Scrub cover (species and percentage cover) in an expanded 10x10m quadrat.
7. Bare ground (percentage cover).
8. Stones, i.e. flint or chalk fragments (percentage cover).

The rabbit survey method (4) is based on that developed by Dolman & Sutherland (1992). The number of eight day old pellets was assessed using a reference set of fecal pellets which were collected from grassland at a known age of eight days, photographed and sprayed with fixative to prevent further desiccation and biodegradation. Photographs and a phial of reference pellets were carried in the field to aid identification.

Sward height during key stages in butterfly life-cycles is known to be important for many species (Oates 1995), but detailed assessments for each species would have been prohibitively time-consuming. Sward height therefore was taken as the final (summer) height of herbaceous growth and was intended to be used as an index of the product of soil productivity, grazing pressure and to some extent grass species composition (and therefore vegetation community). However, the relationship between final sward heights and heights at growth stages in the spring and summer at Porton Down was investigated in 1998 (see Sections 2.8.2 and 3.4).

Sward height assessment (5) was carried out using a 'drop disk'. This consisted of a 30cm diameter wooden disk weighing 200g with a 1.5cm diameter wooden dowel passing through a hole in its centre. The dowel was marked at 1cm graduations excepting 0-10cm which were marked at 0.5cm graduations. The end of the dowel was placed on the surface at the sample point, the disk was dropped from a consistent height of 1m and allowed to settle on the vegetation and the height of the disk above this level was recorded.

In 1995, at alternate quadrat sample points along the transect (usually points 2, 4 etc), a botanical assessment was carried out in the 1x1m quadrat. All higher vascular plants were

recorded with an estimate of percentage cover within the quadrat. Also, percentage cover of bryophytes and lichens as taxonomic groups was recorded as were key species (e.g. *Cladonia furcata* or *Pseudoscleropodium purum*) where identifiable. This was important for NVC classification purposes.

Other notes on grazing stock type and numbers, presence of ant-hills and other potentially important features were also taken.

Standard recording forms were used for botanical, physical feature and management recording (see Appendix 3). Other features were recorded on a separate form (see Appendix 4).

At the end of each sample transect, an overall assessment was made of cover-abundance of all higher vascular plant species, plus bryophytes, lichens, bare soil, stones and litter. This was carried out using the 1-10 Domin scale (Dahl & Hadac 1941) shown in Table 2.6. The assessment was based on the 200x5m butterfly recording band except for scrub cover which was based on an expanded 200x10m area.

Due to the amount of time taken to carry out the habitat and environment assessments using the above methods, in 1996 and subsequent years, only the overall assessments were made of habitat and environmental variables in the transect bands. Slope and aspect were recorded as upper and lower limits or one mid-range value if there was little variation.

Table 2.6: The Domin Scale

Domin Score	Cover-abundance Equivalent
1	<4 percent cover, one or few individuals
2	<4 percent cover, several individuals
3	<4 percent cover, many individuals
4	4-10 percent cover
5	11-25 percent cover
6	26-33 percent cover
7	34-50 percent cover
8	51-75 percent cover
9	76-90 percent cover
10	91-100 percent cover

2.4.2 Larval Food-plants

The abundance of preferred butterfly larval food-plants was assessed from field data sheets *post hoc*. A list of larval food-plant species was compiled from several sources (BUTT 1986; Pollard and Yates 1993; Dennis 1992) and is shown in Appendix 5. Many have multiple larval food-plants but the final list for each species was chosen to reflect the habitat and known plant species abundance at Porton Down. This meant that some perceived commonly used plant species were not included.

For two species, meadow brown and marbled white, it is known that the larvae use a number of grass species, with larval instars moving from the finer grasses to coarser grasses as they develop and grow larger (BUTT 1986). For these two species, the total number of grass species in the vegetation sample was used as a surrogate for larval food-plant diversity.

2.4.3 Nectar Sources

The abundance of preferred nectar source plants was also assessed from field data sheets *post hoc*. A list of nectar source plant species was compiled mainly from BUTT (1986) and is shown in Appendix 6.

2.4.4 Grazing

Stock grazing was also recorded as an environmental variable. Number and type of stock was recorded on the field data forms for later assessment. Many sample areas had been grazed by stock in the previous winter or few months; where this management was known, this was also recorded.

Only the presence or absence of grazing was used in the analyses. Previous (e.g. winter) grazing was not distinguished from current for this purpose although timing of grazing is known to be important (Oates 1995).

2.4.5 Landscape Variables

A number of variables were used to examine the relationship between populations/metapopulations and landscape scale features. The selection of these variables was based on Hanski's (1999) premise that the two most important effects in metapopulation dynamics are patch area on extinction and patch isolation on colonisation (see Section 1.2.3 'Metapopulation Dynamics').

Patches were defined after Hanski and Gilpin (1997) as "a continuous area of space with all the necessary resources for the persistence of a local population and separated by unsuitable habitat from other patches". For Fragmented Sites, patches were delineated usually by clear boundaries between calcareous grassland and scrub of varying quality and surrounding farmland or other very different habitats. Where historically large areas were sub-divided, there was at least "some tens of metres of unsuitable habitat" (such as mature dense scrub) (Hanski 1999) between patches. On Porton Down, the definition of 'unsuitable' habitat by Hanski and Gilpin (1997) above was somewhat re-defined as 'poorly defined habitat between well-defined uniform patches of calcareous grassland' where clearly unsuitable habitat (such as mature scrub) was not obvious. In practice, such areas were those remaining after uniform areas of particular NVC communities and/or areas of uniform structure (e.g. tall *Bromus erectus* grassland) had been delineated.

2.4.5.1 Patch area

On Fragmented Sites, patch area was defined as the total area of grassland of any type. Patches of scrub were included in this definition as long as the scrub was growing amongst grassland and was clearly a contemporary successional feature.

On Porton Down, patches of uniform calcareous grassland NVC types were mapped for the ECN project under contract by Dr P Wilson of Wessex Environmental Associates in summer 1996. These NVC boundaries were added to habitat features of known structural uniformity (mainly areas of scrub, rank and very short grassland), and these were delineated as composite maps. Only clearly defined patches were selected which would stand out either floristically and/or structurally from the surrounding vegetation.

Patch areas were either previously determined on many Fragmented Sites by McSweeney (1991) or were estimated for these sites and Porton Down patches using a 'dot and square' transparent overlay where e.g. each dot represented 0.04 ha for 1:10,000 scale maps and each square 1 ha.

2.4.5.2 Isolation

For Fragmented Sites, measures involving both the distance from Porton Down (the potential major 'source' site – see Section 1.6) and the average distance from each patch to all other patches were used (see Section 2.5.3.1).

For measures within Porton Down, equivalent measures were used which involved the distance of each patch to the nearest major concentration of the species being analysed ('population nodes') and the average distance of each patch to all such nodes. This latter measure replaced that involving distances to other patches as it was felt this would be intuitively more important given the potential fluidity of movement between patches.

2.5 STATISTICAL ANALYSIS

2.5.1 Butterfly Counts

Total counts for each species were recorded for each 200m transect. Where transects were less than 200m, counts were standardised to 200m by

$$N = n.(200/L)$$

where n = unstandardised count,

L = length of transect

For calculations involving means, (standardised) counts were log (+1) transformed using natural logarithms, and these geometric means were back-transformed.

Butterfly data were initially entered onto EXCEL spreadsheets for export to other software packages.

2.5.2 Environmental Variables

Transect sward height was calculated as an average value of means of measurements at each sample quadrat.

Transect rabbit fecal counts were averages of counts at each sample quadrat. Values were calculated for each sample 'nest' and age estimation (see Section 2.4.1).

Examination of both sward height and rabbit fecal counts revealed inconsistencies in types of frequency distribution. Within data sub-sets, some frequency distributions for sward height were normal, some logarithmic in character. Clearly these distributions were strongly related to grazing pressure and the grass species involved. For rabbit fecal counts, some frequency distributions were near-normal, others showed a more square-root distribution. It was therefore decided that each data set should only be transformed if the final grouped frequency distributions showed a clear overall pattern and only if parametric analyses were being performed. For calculations involving means, untransformed data were used.

Aspect descriptions were re-coded to reflect the 'degree of southerliness' of the transect. Thus, north was coded 1, north-north west and north-north east 2, north west and north east 3 and so on to south which was coded 9. This avoided circularity, giving equal weight to both westerly and easterly aspects and maximum weight to warmer and sunnier slopes.

Median values were used for both slope and aspect where 'average' values were required within patches with >1 transects.

Values based on Domin scores proved problematic when average or additive scores were calculated such as calculating mean scores within patches with >1 transects or where total cover-abundance values for all food-plants were required. Several attempts have been made to transform Domin scores for these sorts of calculations (see Bannister 1966; Currall 1987), but these use mid-ranges of transformed percentage cover-abundance values. Averaging is a common way of dealing with rank scores such as Ellenberg Indicator values (see for example, Mountford *et al* 2000). It was felt that it was better to under-estimate combinatory scores rather than over-estimate so the following rules were applied:

Average scores: scores below 4 were assessed according to their directly translated value (e.g. 2 = < 4 percent cover with a few individuals), then 1+1 = 2; 2+2 = 2; 3+3 = 3; but 4+3 = 4 (significant area covered); then rounded down medians were used e.g. 4+5 = 4, 5+6 = 5, but 5+6+7 = 6.

Additive scores: scores below 3 summed to the single highest score (e.g. 2+2+1+1+1 = 2). Thereafter 3+3 = 4 and 4+3 = 4 but 4+4 = 5, 5+5 = 6 etc and 5+6 = 5. It can be seen from Table 2.7 that this works quite well for all combinations excepting 6+6 and 8+8 and above although the latter are not likely to truly approach 'saturated' cover and were not often encountered in samples.

Table 2.7: Additive Domin Scores

Domin Scores	Cover-abundance Equivalent	Additive Score
1+1	<4 percent cover, one or few individuals	No change
2+2	<4 percent cover, several individuals	No change
3+3	<4 percent cover, many individuals x 2	4-10 percent cover
4+4	(4-10)+(4-10) percent cover	11-25 percent cover
5+5	(11-25)+(11-25) percent cover	26-33 percent cover
6+6	(26-33)+(26-33) percent cover	34-50 percent cover
7+7	(34-50)+(34-50) percent cover	51-75 percent cover
8+8	(51-75)+(51-75) percent cover	76-90 percent cover
9+9	(76-90)+(76-90) percent cover	91-100 percent cover
10+10	(91-100)+(91-100) percent cover	100 percent cover

2.5.3 Landscape variables

2.5.3.1 Isolation

Hanski (1999) used a measure of patch isolation S_i:

$$S_i = \sum \exp(- \alpha d_{ij}) N_j$$

where the constant α describes how fast the numbers of migrants from patch j decline with increasing distance from the patch, d_{ij} is the straight line distance between patches i and j

and N_j are the population sizes. N_j can be re-stated as $\approx p_j A_j$ where p_j equals 1 for occupied and 0 for empty patch of area Aj.

However, in an earlier study (Hanski 1994) the same author used a simpler measure, the distance of patch i to the average co-ordinates of all patches in the study network. Using appended data from the paper, it was found that the correlation between this statistic and the measure S_i above was very high ($R^2 = 0.79$, $F_{1,48} = 180.37$, $P << 0.001$). These data were gathered extremely intensively on a metapopulation of the Glanville fritillary *Melitea cinxia* and the conclusion must be that for a study where even presence-absence data may not truly reflect patch occupation (due to low or highly variable probability of detection for example), then the average co-ordinate statistic is a highly suitable measure of isolation.

For Fragmented sites, isolation was calculated for each patch using the distance between patch edges as these were clearly defined and such a measure is spatially more realistic.

For Fragmented Sites, a simple straight-line distance (in km) was measured from the nearest boundary of Porton Down to the nearest boundary of the focal site. This was a distance measure which ignored the effects of other sites as stepping-stones or as source sites.

2.5.3.2 Other Distance Measures

For Porton Down, major population concentrations were modelled interpolatively by plotting total transect butterfly counts as a contour map in Systat 5.0, using mid-transect

grid co-ordinates. A negative exponential smoothing model (NEXPO in Systat) was used as this was most appropriate for the poisson nature of the count data (Burrough 1995). Graphical (visual) estimation of the optimum smoother level was used as recommended by Forney (2000). As Porton Down is an elongated site, dummy locations and 0 counts were added in order to make the grid square. This did not appear to affect the models within the core area of surveyed grassland. Maps for the seventeen species with sufficient data are given in Appendix 7 with two examples shown here in Figures 2.3 a & b. Reference should be made to Figure 2.2 for data source points.

Figure 2.3a: Butterfly count contour map for marbled white at Porton Down in 1997, using mid-transect grid co-ordinates and a negative exponential smoothing model (NEXPO)

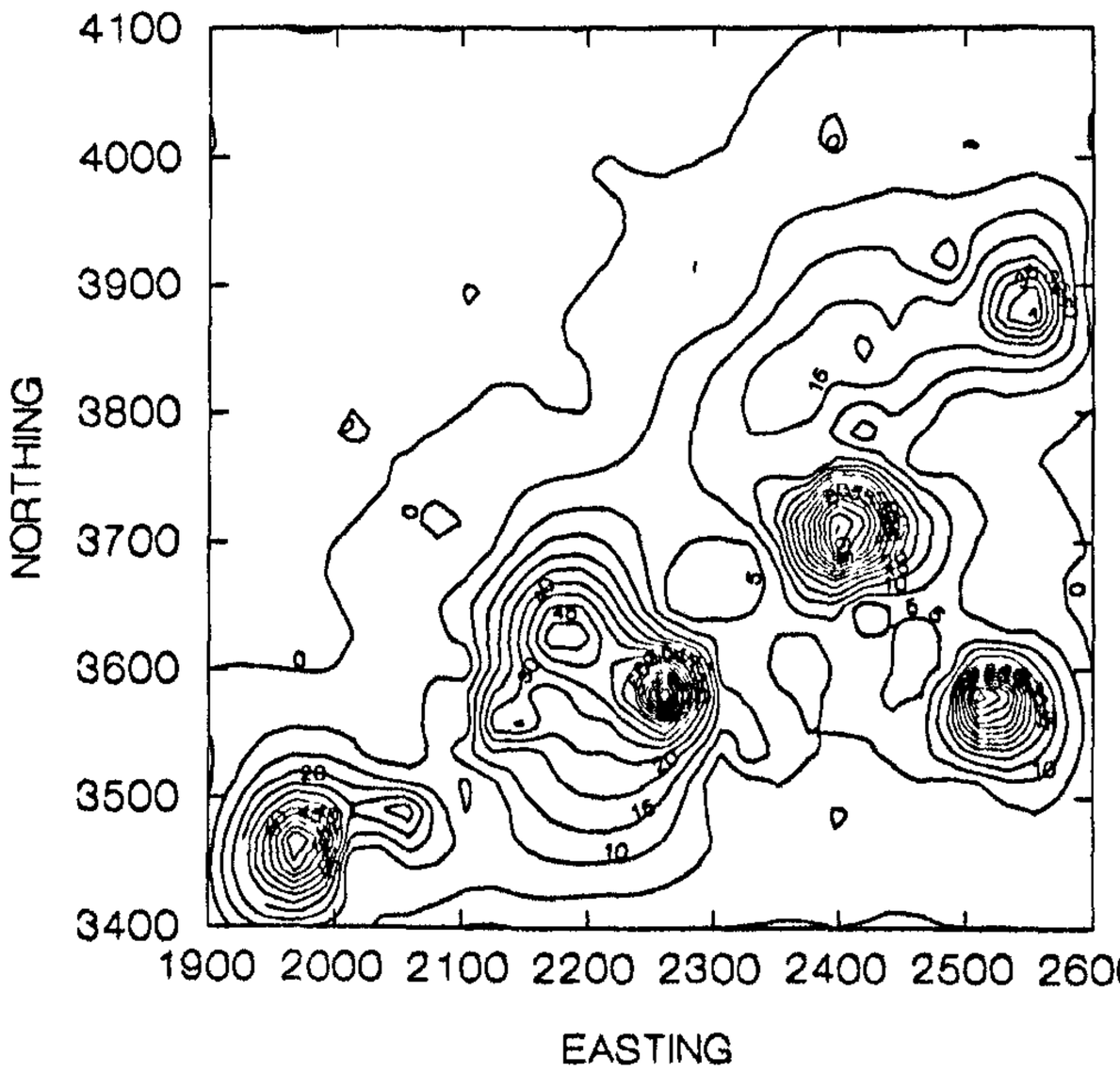
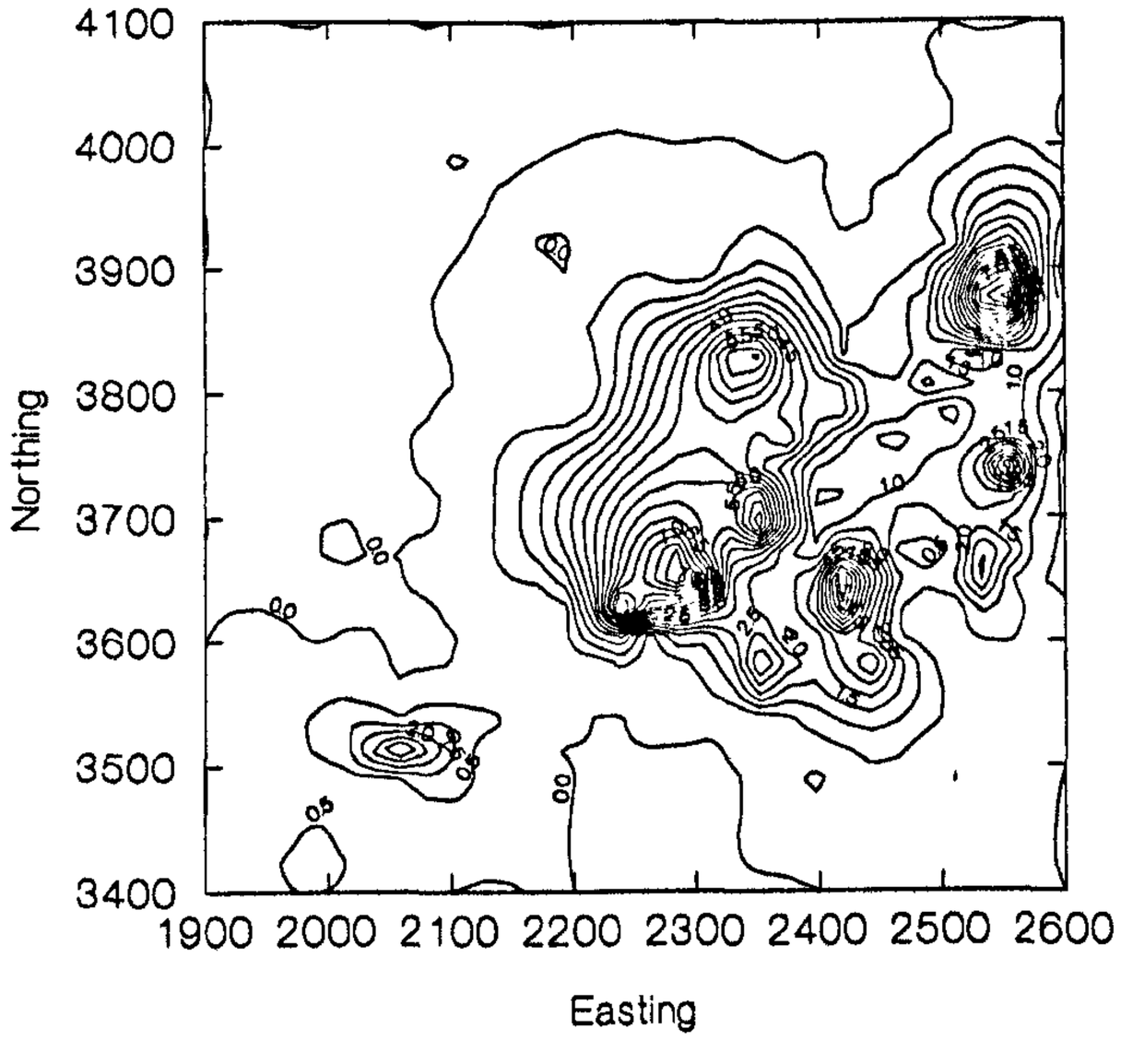


Figure 2.3b: Butterfly count contour map for silver-spotted skipper at Porton Down in 1995, using mid-transect grid co-ordinates and a negative exponential smoothing model (NEXPO)



Centres of major population concentrations ('population nodes') were identified from the major 'peaks' in the contours. These were marked and the distance from these to patches was used for two measures for each species:

1. The distance from the patch centre to the nearest population node.
2. The average distance from the patch centre to all population nodes.

A decision had to be made for some species as to how many population nodes should be used. If a species showed a very patchy distribution with a number of localised population concentrations, all of the nodes with values around the modelled maximum were included. In some instances, a single high value node was used in addition to others of lesser value where it was clear that they stood out from the background values. These high value nodes could not be disregarded (as with outliers in regression models), as they would clearly be able to affect population densities on transects some distance away, particularly in mobile species.

2.5.4 Analysis of Butterfly and Habitat/Environmental Data as Response and Explanatory Variables

SYSTAT 5.0 and 6.0 (Wilkinson 1990; SPSS 1996) were used to perform all of the statistical analyses except those otherwise mentioned.

Analysis of vegetation data was initially carried out using the Vespan III package (Malloch 1995a) which included DECORANA (Hill 1979; Hill & Gauch 1980). DECORANA (**D**etrended **C**orrespondence **A**nalysis) is an ordination method, similar to Reciprocal Averaging, but where correlations between first and subsequent axes are removed and where the resulting 'arch' effect is avoided.

The program MATCH (Malloch 1995b), together with comparison with NVC tables in Rodwell (1992) was used to assign samples to NVC types. Match gives percentage fit coefficients between sample data and NVC communities and sub-communities.

Multiple regression models were constructed in the Generalised Linear Modelling package GLIM 4 (Francis *et al* 1994) to analyse the relationship between butterfly abundance and explanatory habitat and environmental variables. Response (butterfly presence-absence or counts) variables were modelled using either binary or normal errors depending on sparseness of response data. Sparse data were modelled as presence-absence (binary) while common species were modelled using Adjusted Population Indices (see Section 2.6.1). All data sets were initially modelled using the binary form of response data. Where there was no model convergence through the iterative process, then Adjusted Population Indices were used as the response variable in a normal model.

The form of multiple regression model in GLIM using binary data is the 'logistic' term:

$\log_e [p/(1-p)] = b_0 + b_1x_1 + b_2x_2 + \ldots\ldots b_nx_n$

where $\log_e [p/(1-p)]$ is the logit or probability of occurrence and b_n parameters and x_n environmental parameters respectively. The logit link is used in GLIM (Crawley 1993).

The form of the multiple regression model in GLIM using normal errors is the expression:

$\eta = b_0 + b_1x_1 + b_2x_2 + \ldots\ldots b_nx_n$

where η is the transformed count or estimated population index and b_n constants and x_n environmental parameters respectively. The identity link is used in GLIM (Crawley 1993).

A forward elimination process was used to find the most parsimonious (minimal adequate) model for each response variable using maximum likelihood estimation methods. This proceeded by adding in and then subtracting each of the (x) explanatory variables in turn to

a null model, keeping the variable showing the greatest change in scaled deviance Chi-square (χ^2) value in logistic and the greatest t-value in normal models. The model was then re-run with the new (x-1) data set. The model selected was that which contained all the variables included in the forward process which had individually significant changes in scaled deviance χ^2 values or, for normal models, F-values calculated from change in deviance and scale parameter when each variable was subtracted from the full model (Crawley 1993). The form of model using normal errors includes the Scale Parameter in the modelling process and therefore accounts for overdispersion in subsequent significance tests (K. Vines pers. comm; Crawley 1993). Overdispersion is the lack of a relationship between one or a few environmental parameters and the response variable and meant that the use of poisson errors in the models was problematical (Crawley 1993).

All χ^2 values in logistic models greater than 3.841 (i.e. $P < 0.05$), were allowed in the total model as individual parameter degrees of freedom are unitary. In normal models, t-values greater than that defined for the degrees of freedom relevant to the current model (i.e. 1,(n-(v-1)) where n = total number of explanatory variables and v = number of variables in the model) were allowed in the total model.

Models were fitted using data sets which included discrete NVC categories classified from the Match analyses. As transect samples were relatively large for vegetation sampling, they often covered two or more NVC types. For Porton Down, these were therefore included as binary variables and any one sample could carry several unit scores. For the Fragmented Sites whole patch analyses, areas of NVC types were used (see Sections 2.3.2 and 2.3.3).

Raw data for each explanatory variable were plotted to see if their relationship with the response variable was strongly curvilinear. These relationships are often gaussian in nature and should be incorporated in the model if over-simplification is to be avoided (Jongman *et al* 1995). If this was the case, the square of the explanatory variable was included in the analysis. If, in the minimal adequate model, the coefficient of the explanatory variable was positive and that of its square was negative, then the variable had a gaussian distribution (if the coefficient of the explanatory variable was negative and that of its square was positive, then the variable had an inverse gaussian distribution). If the normal version of the explanatory variable was excluded during the forward process, the square form was also excluded.

The above criteria were also applied to variables consisting of Domin values as they were to be treated in a similar fashion to continuous variables in GLIM. An alternative method would be to treat Domin scores which showed strong curvilinearity as Factors (Crawley 1993; N. Aebischer pers. comm.) but this would have created a large number of explanatory variables and would lead to potential Type I errors (Zar 1984). Ter Braak (1987a) used rank environmental scores as continuous variables in polynomial regression analysis; this is the method employed in CANOCO (see below).

CANOCO (**Can**onical **C**ommunity **O**rdination, ter Braak 1987a) was used to correlate butterfly communities to habitat and environmental variables (see Section 2.4). CANOCO is an extension of DECORANA (Hill 1979), but does not assume linearity in the data, correlates environmental variables with ordination axes and is able to detect unimodal (gaussian) relationships between species and external variables. Using this method, species

occurrences were investigated in relation to ordination axes, where more general patterns of coincidence of several species provides a greater ability to detect species-environment relationships (ter Braak 1987b). The version CANOCO 3.1 was used in this study.

2.5.5 Model Testing

The basic premise was that habitat selection models would be constructed from the Porton Down 1995 data and tested, in terms of predictive power, using the Porton Down 1997 data. Models constructed using the 1995 Porton patch data were tested using the 1997 Porton Down patches. Population 'nodes' (see Section 2.5.3.2) were modelled and used separately for 1995 and 1997 data. There were, however, three scenarios where this was not possible or where additional analysis using the other data sets was required. These were:

i) Due to the unusual climatological nature of the 1995 flight season, particularly during July and August (see Section 3.6), habitat selection behaviour may not have been typical in this year. This would have been manifest when models were tested against the 1997 Porton Down data. In this case, models were produced retrospectively using the 1997 Porton Down data. The predictive power of these models was tested against the 1995 Porton Down data. If the 1997 and 1995 models predicted very different outcomes, then the 1997 model was assumed to be the best as climatological conditions were more 'normal' in that year.

ii) A few species were present in low numbers on sample transects at Porton Down in both 1995 and 1997. However, these species (small and Essex skippers and ringlet), were

relatively common on Fragmented Sites and therefore required local scale habitat models. It was decided that models produced from Fragmented Site transect data would be the only way of describing habitat selection. The caveat here is that there is no way of telling the degree to which isolation and other metapopulation processes might affect the outcome of these models. However, as the species were absent from only a very few Fragmented Sites, it was felt that these models would be adequate to describe habitat selection behaviour on a regional level and at a local scale.

iii) For common blue and chalkhill blue, models produced from Porton Down data were not considered adequate and therefore models from Fragmented Site data were used comparatively. Both of these species were more common on Fragmented Sites and it was felt that models produced from Fragmented Site local scale data might have greater predictive power.

Models constructed from 1996 Fragmented Site patch data were tested using the 1997 Fragmented Sites data set. However, these two sets of sites probably influence metapopulation processes between each other and for this reason, measures such as isolation were calculated using the 1996 and 1997 sites as a single data series.

2.5.6 Intra-set Correlations

Correlations among explanatory variables are a well-known problem in multiple regression analysis (Crawley 1993). The degree of correlation in the 1995 Porton Down data set was investigated initially by normalising data as far as possible by log transforming sward

height and square root (+0.5) transforming rabbit index (fecal pellet count) and examining the Pearson Correlation Matrix. This is shown in Appendix 8.1.

The degree of correlation among the other major data sets used (Porton Down 1997 and Fragmented Sites 1996) was also investigated and these are shown in Appendix 8.2 and 8.3.

Additionally, the data set for each butterfly species which included its larval food-plants and nectar sources as well as landscape variables (where applicable), was examined for high correlations.

Where explanatory variables were 'brought forward' from a local scale to a landscape scale analysis, those variables which were excluded from the final local scale model but were strongly correlated with variables which were included in the model, were added to the modelling process for landscape scale models. This avoided chance exclusions of potentially significant variables due to multiple correlations.

The recommended method for dealing with strongly correlated variables is to model them as individual variables and as products (Crawley 1993). One problem with this is that 'global' models which include all possible products will lead to over-parameterisation (Mauritzen *et al* 1999). Only products of strongly correlated variables ($r > 0.5$) were therefore included and as long as there was a logical biological meaning to them. This was carried out as required for each data set when regression analyses using GLIM4 were run.

In exceptional cases, highly correlated variables which were of low frequency were used additively as well as product parameters. This prevented product parameters becoming largely series of zeros.

2.6 CUSTOMISED ANALYSES

2.6.1 Butterfly Data

For each butterfly species, a matrix of transect (row) by visit date (column) data was entered on a spreadsheet. Weekly population index data were recorded independently on the ECN BMS transects, enabling population curves to be drawn which were smoothed by eye. Attempts to super-impose model curves on these data were not successful as 'least squares' methods could not be made to fit well even at high level polynomials. Methods for fitting curves to these data are being developed by statisticians at CEH Monk's Wood and CEH Merlewood (A. Scott and N. Greatorex-Davies both pers. comm.) for interpolating BMS counts and calculating residuals of population curves. Zonneveld (1991) had some success fitting simple curves to butterfly count data in order to estimate death rates but these were largely single emergence, univoltine species.

As research survey data represented between one and six dates during the flight period for any one sample transect, a method needed to be found whereby these sparse data could be corrected for the point in the flight period when the survey date was super-imposed on the population curve (see Figure 2.4a).

In notation, and referring to Figure 2.4a (stylised BMS monitoring population curve) and Figure 2.4b (stylised example research transect population curve):

If t = the sampling date, I_t = the BMS count on day t, P_t is the research transect count on day t, then

$$P_t = c^* I_t$$

Where $c = \dfrac{\sum P_t}{\sum I_t}$ and standard error of c is $\pm \sum P_t / \sum I_t$

Assuming a Poisson distribution and $\bar{P} = c * \bar{I}$

NB: Standard error was arrived at by maximum likelihood estimation (K. Vines, pers. comm.).

Figure 2.4a: Stylised BMS monitoring population curve.

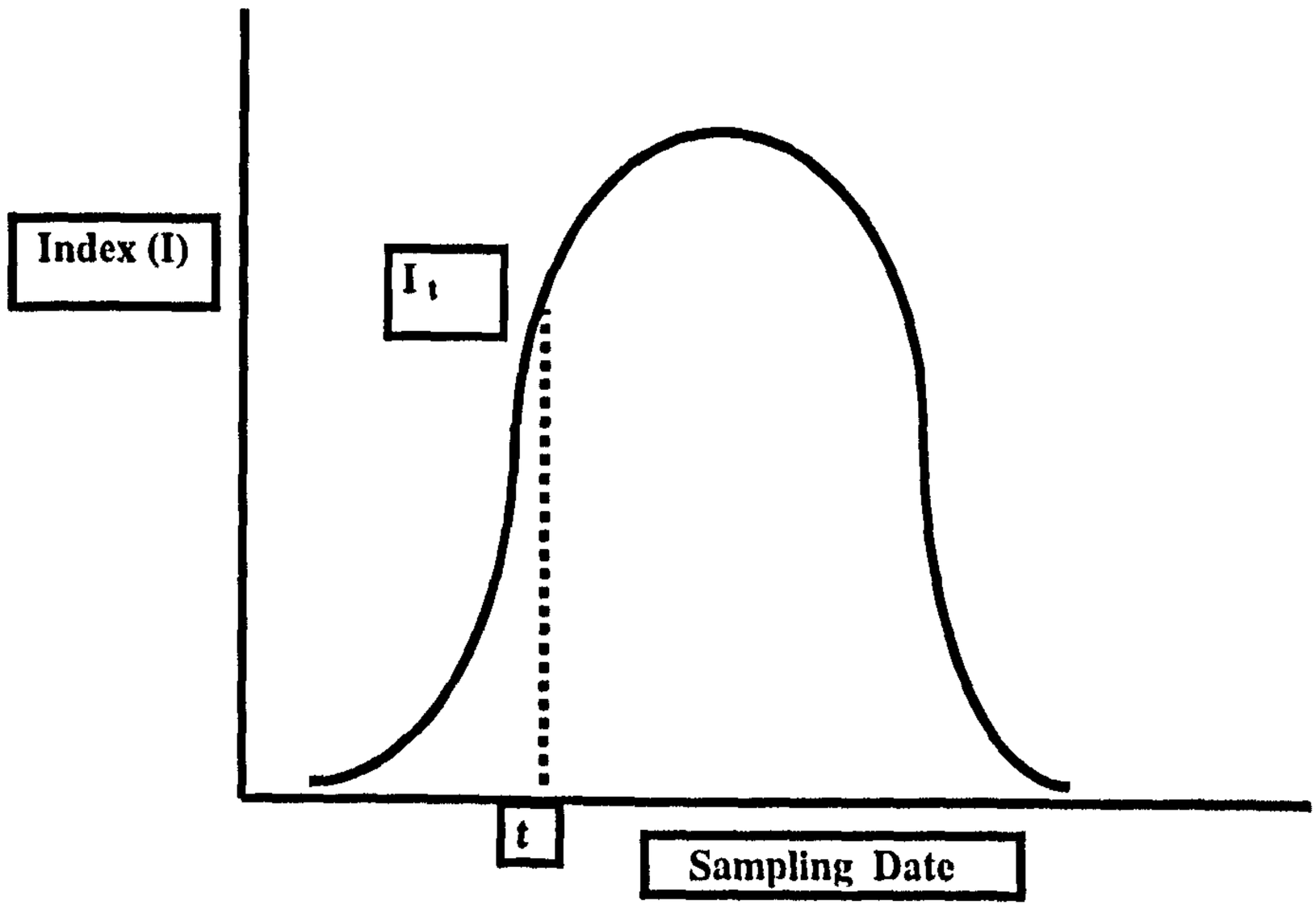
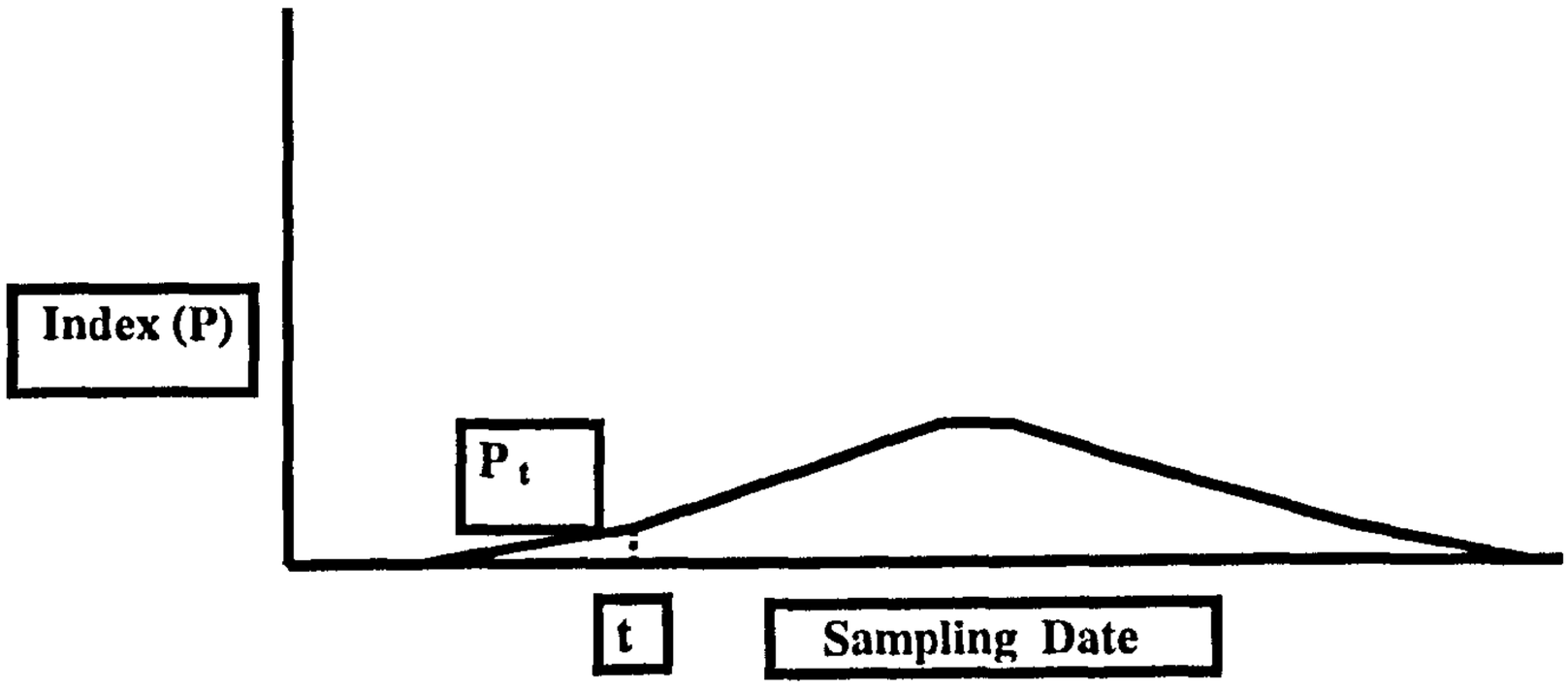


Figure 2.4b: Stylised example research transect population curve.

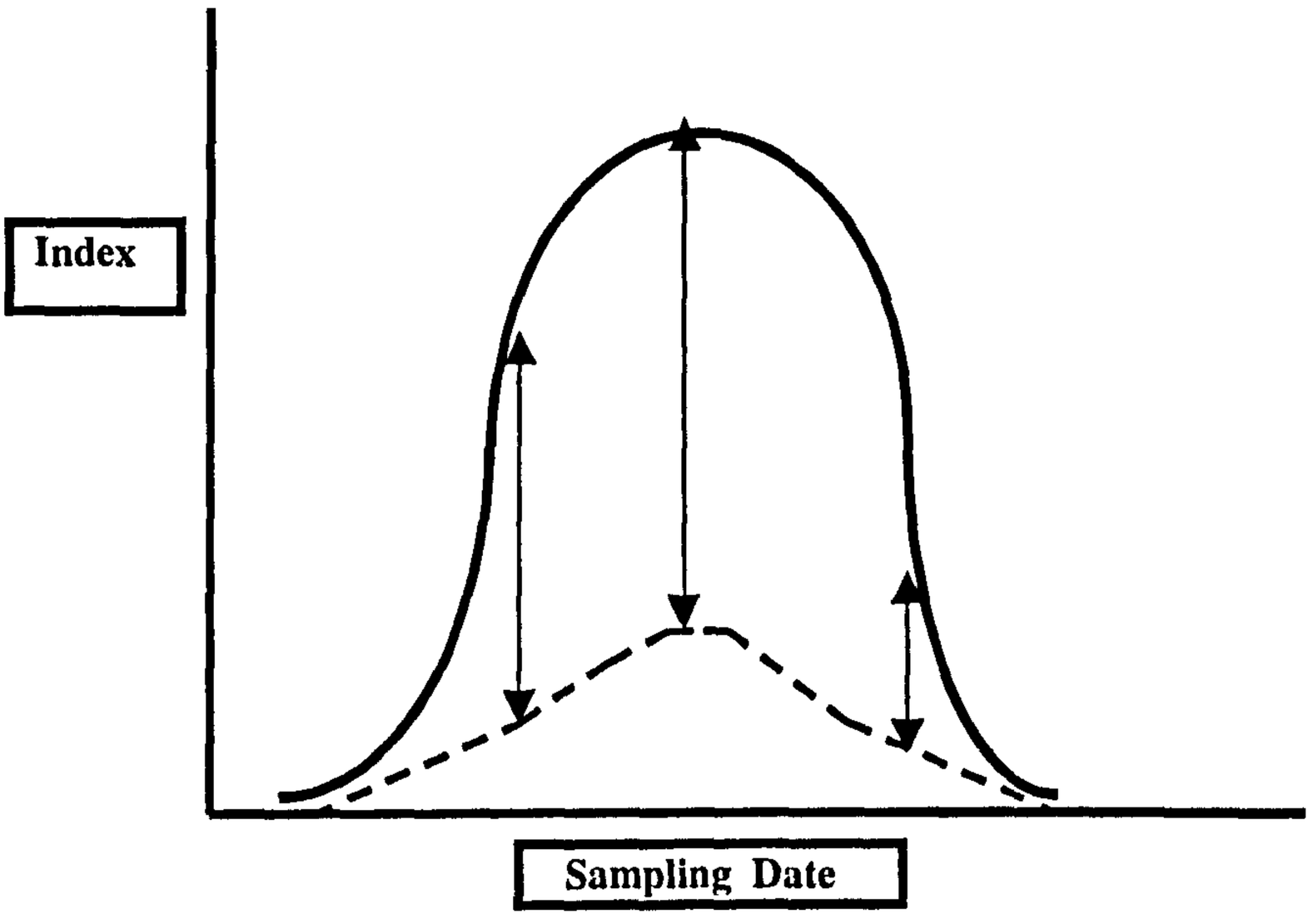


Over all sampling dates in a flight period, each arrow showing the difference between the BMS count and research transect count on day *t* in Figure 2.4c would therefore approximate to P_t / I_t .

Instead of attempting to calculate the area under the curve to arrive at $\sum I_t$, the local Porton Down BMS population index was used, as explained in Section 2.2.2.

Results from these adjusted estimates correlated strongly with summed total counts for all five species concerned (Figures 2.5a to 2.5e). Values for $R^2 adj.$ were: common blue 0.591; dark green fritillary 0.786; marbled white 0.955; meadow brown 0.939; small heath 0.872. The two data sets were not independent and these figures therefore simply give an indication of variance between 'source' data and modelled data. Errors for common blue were relatively large. This was probably due to the high index for the second generation which would produce greater errors when sample transects where recorded by chance towards the ends of the population curve.

Figure 2.4c: Illustration of relationship between BMS and research transect counts on sample days.

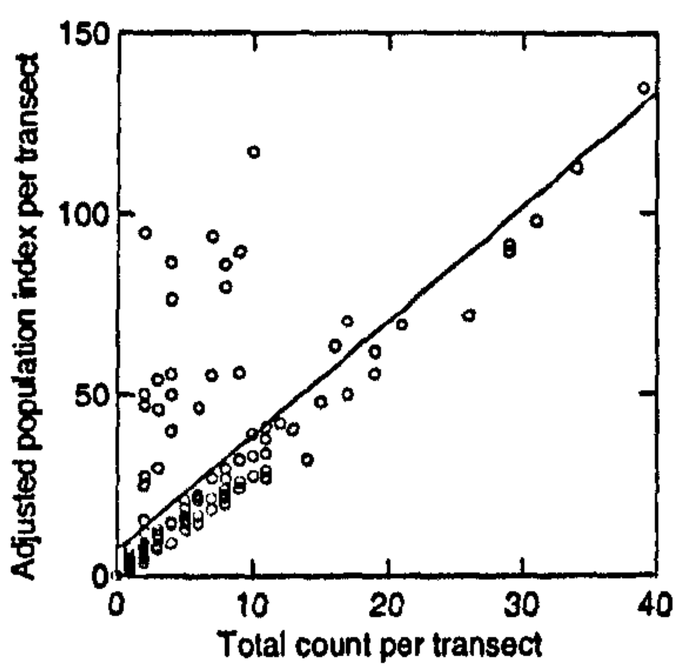


A test of the statistical power of this method was performed on data for the meadow brown using Porton Down BMS transect data and is shown in Appendix 9.

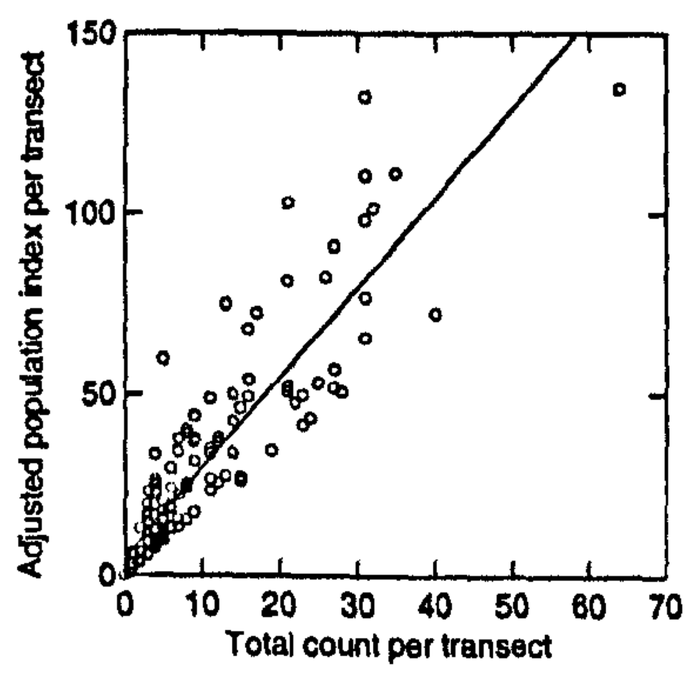
Population data from the Porton Down BMS transects were also used to calculate indices for transects on Fragmented Sites for common blue, marbled white, hedge brown and meadow brown. These species were very common and had to be modelled using generated 'count' data. These indices were then used for regression analyses only (see Section 2.5.4). The assumption that population curves at Porton Down would closely reflect those on Fragmented Sites was tested using data from Broughton Down and Dean Hill, two of the study sites, and also Martin Down, a large chalk grassland site some 10 km west of the

Figure 2.5: The relationship between adjusted population index and total count per transect for a) common blue, b) dark green fritillary, c) marbled white, d) meadow brown and e) small heath. All data are for 1995.

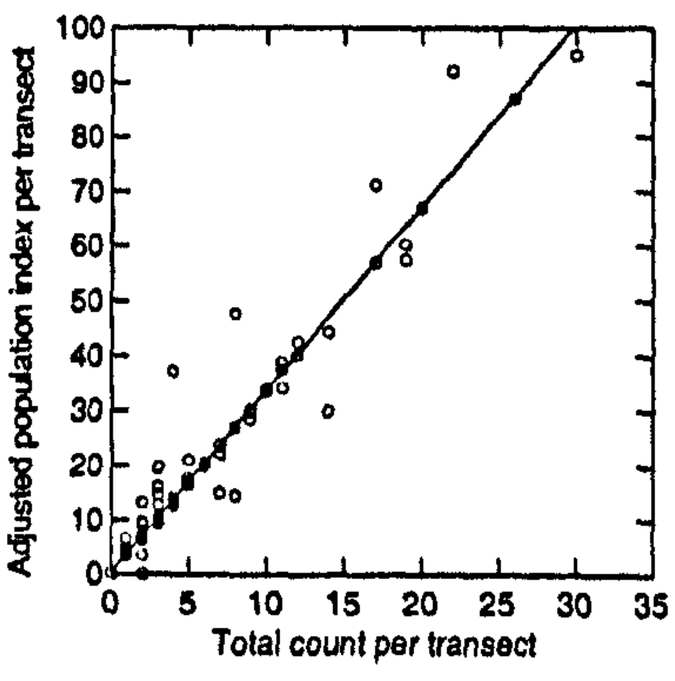
a)



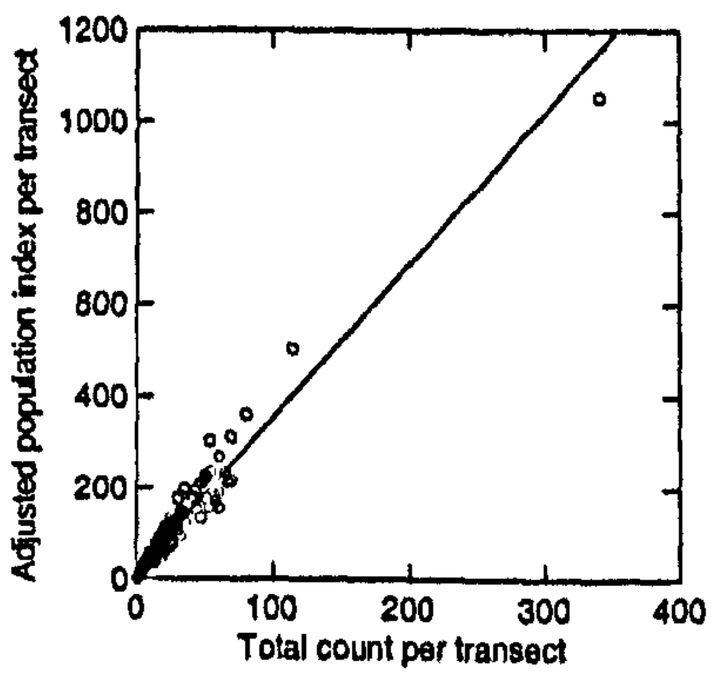
b)



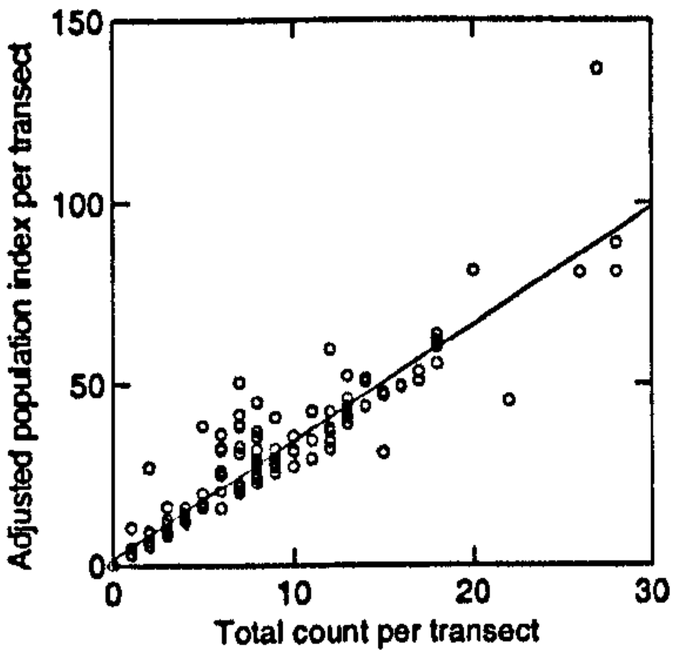
c)



d)



e)



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study area boundary. If a high, or sufficient degree of correlation could be found between the within-year population curves on Porton Down and these sites, then the index calculation method could be used.

In fact, strong within-week correlations were found for marbled white, hedge brown and meadow brown (all $P \leq 0.001$). For common blue, the correlation was weaker ($0.01 > P > 0.001$) due to differences in first generation indices, but was felt sufficiently strong for the method to be used. The full results of the tests are given in Appendix 10.

2.6.2 Data Used in CANOCO Analyses

Total count data were used in all CANOCO analyses as there was a requirement for comparative quantitative data for all species (to sufficiently distinguish between common species occupying similar habitats) and the adjusted estimate method (above) showed that total counts were reasonably well correlated to modelled population estimates.

2.7 INCIDENCE FUNCTION MODELS

The Incident Function Model (IFM) has two main functions in metapopulation modelling. Firstly, it provides parameters relating to the stochastic processes observed in the metapopulations being modelled. Secondly, it uses these parameters to model incidence (patch occupancy and turnover) on the patch network. In this study, the main interest is in the relationship between the metapopulation parameters (relating to minimum patch area, degree of environmental stochasticity, colonization ability and the effect of distance on dispersal) and the landscape level model parameters arising from GLIM regression analyses.

The IFM is a discrete-time stochastic patch model, a metapopulation level extension of a first order linear Markov chain model for an individual habitat patch (Hanski 1994 &1999). The model is fitted to presence-absence data from a set of habitat patches to estimate a series of parameter values, which then allow numerical iteration of metapopulation dynamics in other systems of habitat patches. If J_i is the stationary probability that patch i is occupied, then this 'incidence' can be described by

$$J_i = \frac{C_i}{C_i + E_i} \qquad (2.1)$$

where E_i and C_i are extinction and colonization probabilities.

Transition probabilities between the two states E_i and C_i are functions of patch area and isolation as defined by

$$E_i = \frac{e}{A_i^x} \qquad \text{if } A_i > e^{1/x} \qquad (2.2)$$

$$E_i = 1 \qquad \text{if } A_i \# e^{1/x} \qquad (2.3)$$

where A_i is the area of patch i and e and x are two constants, and

$$C_i = \frac{M_i^2}{M_i^2 + y^2} \qquad (2.4)$$

where M_i is the number of immigrants into patch i and y is a parameter which determines how fast the colonization probability approaches 1 with increasing M_i. This function gives an s-shaped increase in the colonization probability from 0 to 1 with increasing numbers of immigrants.

Two further effects are taken into account in developing the full model. Firstly there is the rescue effect (see Section 1.5), which is the decrease in the risk of local extinction due to the raised level of immigration from a patch with a large population. This reduces the extinction probability to $(1 - C_i)E_i$ and equation 2.1 above becomes

$$J_i = \frac{C_i}{C_i + E_i - C_iE_i} \qquad (2.5)$$

Assuming also that the isolation effect is a function of distance between patches, patch area and population, given by the equation

$$S_i = \sum \exp(- \alpha d_{ij}) N_j \qquad (2.6)$$

then the following expression describes the incidence of patch i

$$J_i = \frac{1}{1 + \frac{ey}{S_i^2 A_i^x}} \qquad (2.7)$$

Parameters e and y can be separated by defining a minimum patch area A_0, for which the extinction probability in unit time is 1, $E_t = 1 = e/A_0^x$, from which $e = A_0^x$ (Hanski 1994).

The model parameters and their meaning can be summarised as follows:

J is the long-term probability of patch occupancy.

e and x are parameters of annual extinction probability E as a function of patch area $E = e/A^x$.

x reflects the effective strength of environmental stochasticity and the value decreases with increasing environmental stochasticity.

y describes the colonisation ability of a species. Good colonisers which are little affected by isolation have small y values.

- α is the effect of distance on dispersal. The quicker the drop-off in a species' dispersal ability, the greater the value.

S describes patch isolation as a function of distance to, and occupancy of patches in a network. Large values of S correspond to small isolation.

A_0 is the critical minimum patch area where extinction probability in unit time is 1.

Parameters were estimated by maximum likelihood methods (Moilanen 1999). Models were provided by the University of Helsinki Metapopulation Study Group and were downloaded from their web-site (*www.helsinki.fi/science/metapop*). Two stages of modelling were required. Firstly, a relatively quick estimation, using the NLR (Non-Linear Regression) method, gave an approximation for parameters. It was important that 'seed' values were reasonable estimates, otherwise parameter estimation varied greatly. These were taken from published (mainly Hanski 1999) and unpublished (R. Wilson,

Leeds University *pers. comm.*) sources. This method also gave an estimated patch turnover rate. These values were then put in another model which used implicit statistical inference and Monte Carlo estimation methods (Moilanen 1999). Ten model runs were made to provide a mean estimate and errors for each requested parameter.

Adaptations were made to the data to run the models. Firstly, Porton Down, which was included as part of the modelled patch network, was split into seven patches of < 100 ha and observed presence-absence of the focal species in these patches was used. The reasons for this is as follows (Moilanen pers. comm):

1. A very large patch would have a zero extinction probability (possible for some species, unlikely for many).
2. It would also produce a huge number of migrants which would cause many patches in the network to be occupied all of the time.
3. The metapopulation would persist forever in the modelling sense, and the pattern of occupancy would be greatly distorted.
4. Parameter estimation over a very wide range of patch areas and isolation would cause problems in terms of function fitting.

Clearly, a large 'mainland' patch such as Porton Down does not exert influences in direct proportion to its relative size.

A limitation also exists on the species which could be modelled using the IFM. Hanski (1994) recommended that the fraction of occupied patches for the species should be greater than 0.2 and less than 0.8. Under this criterion, only seven species qualified from

the Fragmented Sites. These were grizzled skipper, dingy skipper, green hairstreak, small copper, brown argus, chalkhill blue and dark green fritillary.

One important assumption in the IFM model is that populations are at equilibrium (Moilanen 2000). However, this is not quite so important when parameters are being estimated rather than modelling patch occupancy. If sampled metapopulations are not at 'stochastic quasi-equilibrium' then trends in metapopulation size will result. For the purpose of this study, only relative parameter estimates were required and any error due to sampling in one year would not be critical.

As an assumption of population stability is implicit in the use of the IFM in this study, the data for Fragmented Sites surveyed in 1996 were added to those from 1997 to give as complete a picture of the Fragmented Site metapopulation as possible.

2.8 OTHER DATA CONSIDERATIONS

2.8.1 Rabbit Index Data

Data on the number of rabbit fecal pellets were recorded on a nested quadrat basis adapted from the method of Dolman & Sutherland (1992) as explained in Section 2.4.1. This method required the estimation of the number of fecal pellets less than 8 days old. In practice, distinguishing between fecal pellets less than 8 days old and older ones proved to be extremely difficult. This was because old pellets could take on the appearance of ones less than 8 days old when wet after rain and if they were still intact. It was felt that this may have produced unacceptable error in the data.

In order to investigate an adequate alternative method, data from 354 of the 356 quadrats recorded in 1995 were analysed. It was assumed that a) decay rates for rabbit fecal pellets were constant between sample areas and across sample dates, b) measured sward height was strongly correlated with the number of rabbits present and c) rabbits produced approximately constant numbers of fecal pellets with time and across habitat types.

2.8.2 Assessing Sward Height Changes

The rationale behind the vegetation sampling in this study is to obtain relative measures of vegetation characteristics as explained in Section 2.4.1. However, many detailed studies of butterfly biology have found relatively narrow limits of tolerance to sward height at key stages of development (see for example, Thomas 1983). In order to better understand how the single measure of sward height relates to seasonal sward heights, it was decided to sample selected transects which experienced different grazing pressures. 40 transects were selected and sward height was measured at 10 points along the transect, starting at 10 metres in from the end (i.e. at 10, 30, 50....190 m). This would ensure that as far as possible, the same vegetation patch was measured at each sampling period. These transects were measured in May, June, July, August, September and October 1998 to co-incide with the main butterfly monitoring period (May-September inclusive) and the main vegetation sampling period during 1995-1997.

Transect averages were calculated for the ten samples. Samples were ranked according to relative rabbit grazing pressure into 3 (high), 2 (medium) and 1 (low grazing pressure). Ranking was done according to mean numbers of rabbit fecal pellets per transect, where 0-50 was low, 51-150 medium and 151+ high grazing pressure. Transects were grouped

according to rabbit fecal data gathered over the three sample years at Porton Down and therefore there would have been some local differences compared to 1998 due to changes in rabbit populations.

2.8.3 The Relationship Between Adult Butterfly and Larval Populations

The basic premise tested in this study is that adult butterfly population samples closely reflect their use of the habitat for breeding purposes, i.e. adult/egg/larva numbers are closely correlated. It might be, for example, that some adults, particularly of highly mobile species, were using particular habitats for nectaring and these habitats were entirely unsuitable for breeding purpose.

To test this, a mobile species, dark green fritillary, was selected. Adult (adjusted population indices) were available for sample transects. 20 of the 1997 transects were randomly selected and sample points were selected at 20m intervals as in Section 2.8.2 above. Transects were walked during the period 29 July to 5 September after the larvae had finished their initial development phase. The nearest patch of larval food-plant *Viola hirta* was located from these points and the number of leaves in a $1m^2$ quadrat were counted. The number of leaves predated by dark green fritillary larvae was then counted in the same patch. The ratio

No. predated leaves/Total No. leaves in sample

gave an index of larval activity.

In 1998, a similar method was applied to the silver-spotted skipper. In this case, an attempt was made to count egg numbers in samples based on the sampling strategy above.

However, eggs were extremely difficult to find and after 10 sample transects this part of the study was abandoned. The reason for the scarcity of eggs was probably that suitable egg-laying habitat is relatively widespread on Porton Down and the method devised was not intensive enough to count eggs at such a low density.

Small blue

Picture: Simon Coombes

3. GENERAL RESULTS

3.1 DATA SETS

There were five data sets available for producing and testing baseline models from transect data. These were:

a) Porton Down 1995 (60 transects)

b) Porton Down 1996 (20 transects)

c) Porton Down 1997 (67 transects)

d) Fragmented Sites 1996 (94 transects)

e) Fragmented Sites 1997 (25 transects).

The transects sampling periods between 1995 and 1997 are shown in Appendix 11.

It was decided that the Porton 1996 data set was probably too small to be useful for producing and testing baseline models and it was therefore not used for this purpose.

3.2 VEGETATION ANALYSIS

DECORANA analysis of both the Porton 1995 and 1997 and Fragmented Sites 1996 data sets were carried out separately using VESPAN III and MATCH (see Section 2.5.4). A DECORANA analysis was run on each data set using a standard run except that rare species were down-weighted. This ensures that rare species do not overly influence the ordinations and cause both species and sample 'outliers' to occur (Hill and Gauch 1980).

The results of the Porton Down 1995 and 1997 and Fragmented Sites 1996 analyses are shown in Figures 3.1, 3.2 and 3.3 respectively. These plots show axes 1 and 2 of species and sample ordinations. Overlaid on the sample ordinations are the results of Match analyses which have assigned NVC types to the samples.

Figure 3.1 shows that the four main calcareous grassland NVC types, CG2, CG3, CG6 and CG7, are clearly separated from the main mesotrophic grassland type, MG1 (plus MG5/6) along axis 1, the major axis. Separation of the calcareous grassland types is along axis 2.

Figure 3.1: Site scores for the first two axes of a DECORANA analysis for the Porton Down 1995 transects

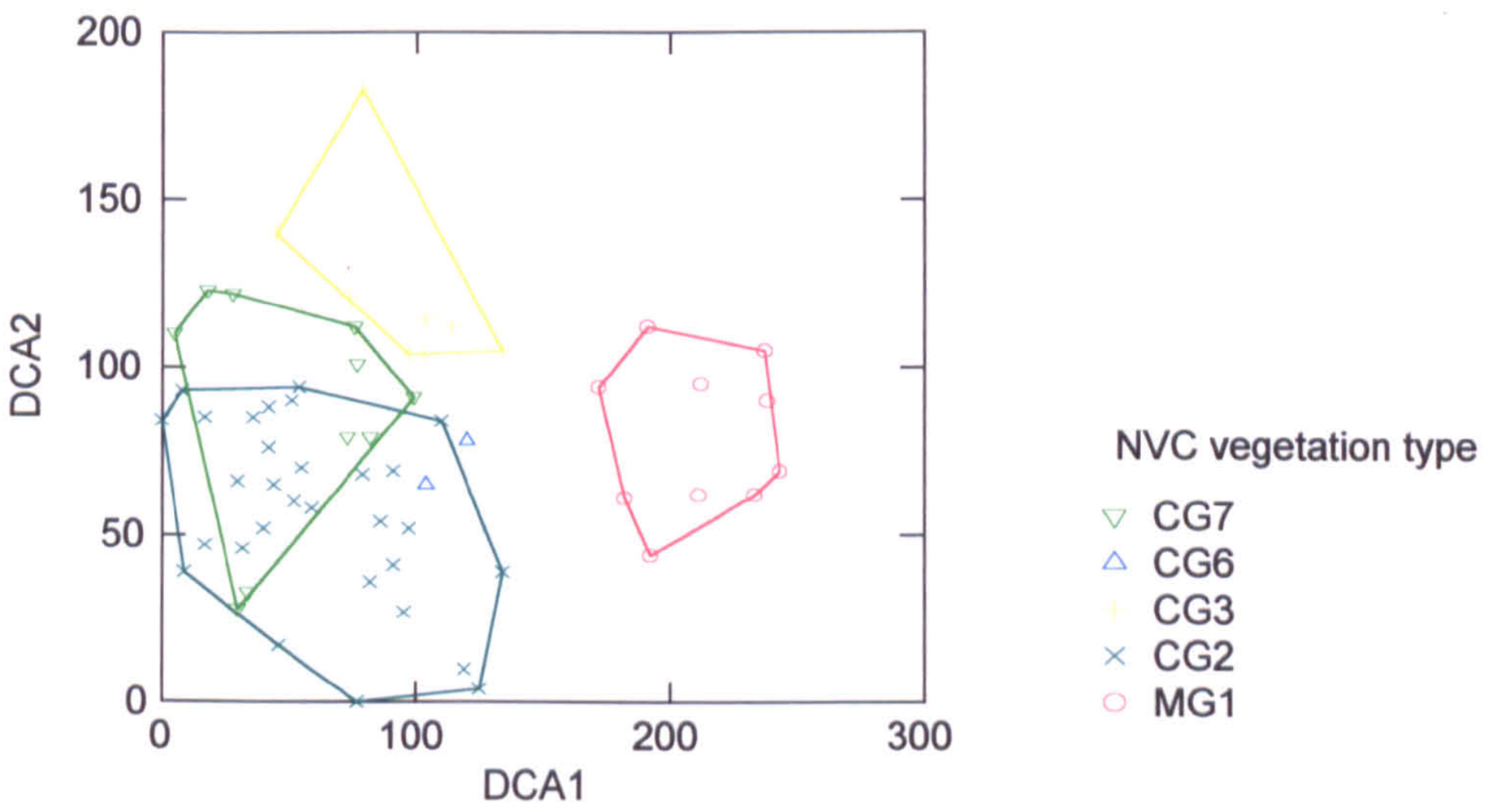


Figure 3.2: Site scores for the first two axes of a DECORANA analysis for the Porton Down 1997 transects

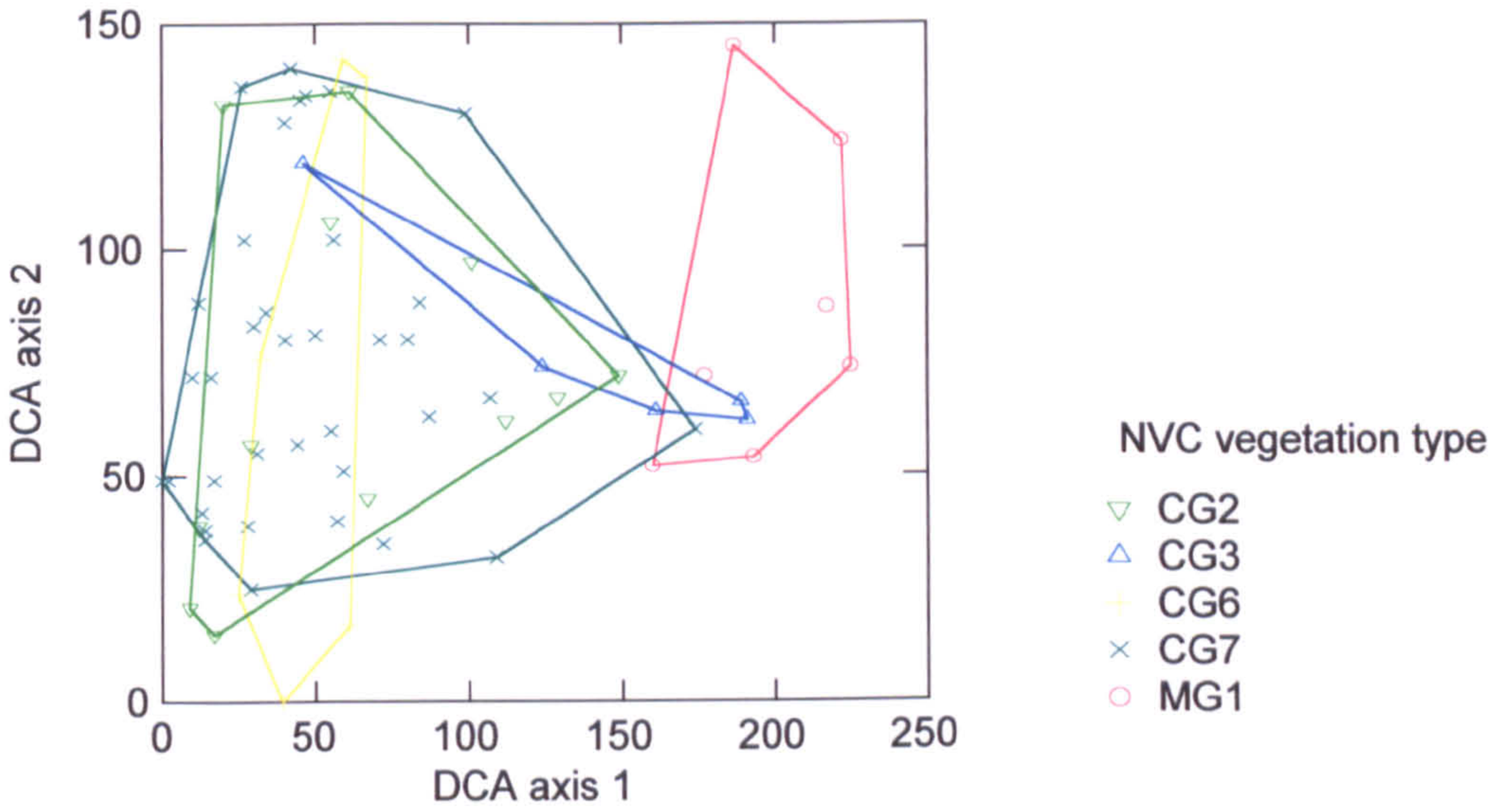


Figure 3.3: Site scores for the first two axes of a DECORANA analysis for the Fragmented Sites 1996 transects

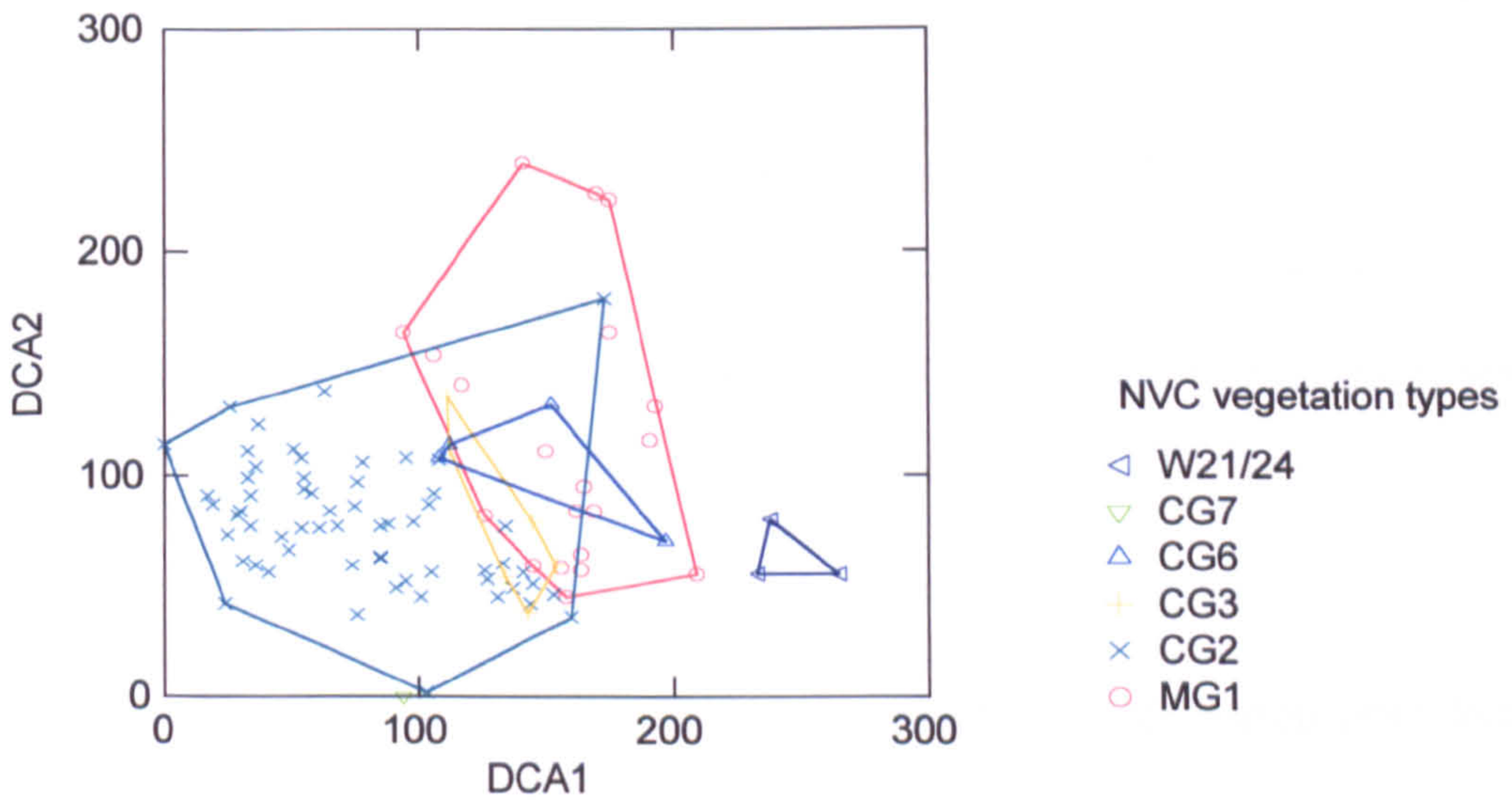


Table 3.1 shows the Spearman rank correlation coefficients between DECORANA Porton Down 1995 site scores and habitat/environmental measures at those sites. Axis 1 is clearly related to sward height in one direction and rabbit grazing intensity, bare ground and stones (which are strongly correlated see Appendix 8.1), in the other direction. This is probably also a function of factors such as soil depth which dictate productivity and therefore vegetation growth rates.

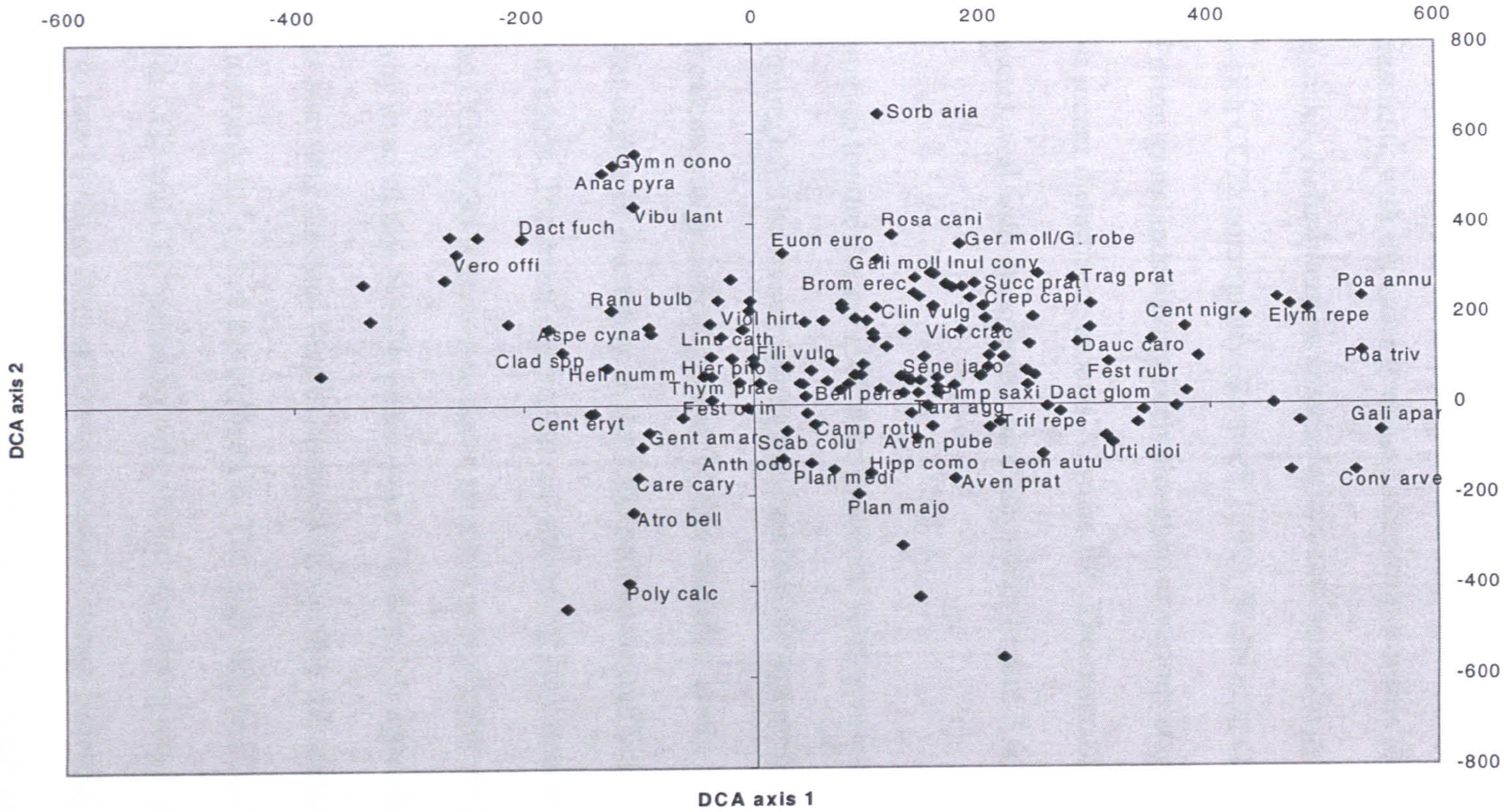
Table 3.1: Spearman rank correlation coefficients between DECORANA site scores and habitat/environmental measures

Variable	Axis 1	Axis 2
Sward height	0.640 ***	0.314 **
Rabbit grazing index	-0.516 ***	-0.332 *
Slope	-0.115	-0.173
Aspect	0.014	0.084
Scrub	-0.189	0.611 ***
Bare ground	-0.498 ***	-0.032
Stones	-0.530 ***	-0.035

Asterisks indicate the statistical significance of correlations: * $P < 0.01$, ** $P < 0.002$, *** $P < 0.001$ ($n = 60$ for all).

The species plots for axes 1 and 2 of the DECORANA ordination of the Porton 1995 data is shown in Figure 3.4. Key species only are notated.

Figure 3.4: Species plots for the first two axes of a DECORANA ordination of the Porton Down 1995 transect data (for species codes refer to Appendix 3).



Gibson *et al* (1991) classified plant species as being associated with early, mid, mid-old and old (> 100 years) stages of succession on calcareous grasslands in southern Britain. Using these classifications as ranks, there is a strong negative correlation between the species scores along axis 1 and their groupings (Spearman rank correlation $r_s = -0.689$; n = 75; $P < 0.001$). There is no correlation with axis 2 ($r_s = -0.071$; NS). Axis 1 is therefore also related to age of grassland, with the older grassland occurring towards the end where species such as *Festuca ovina*, *Helianthemum nummularium* and *Asperula cynanchica* are constants in the species-rich CG2a community (Rodwell 1992). Wells *et al* (1976) found good evidence for the Porton grasslands having been ploughed at various stages in the last 200 years, with the most recent disturbance around 75 years BP. The range of dates determined by Wells relates well with the species' plots shown in Figure 3.4.

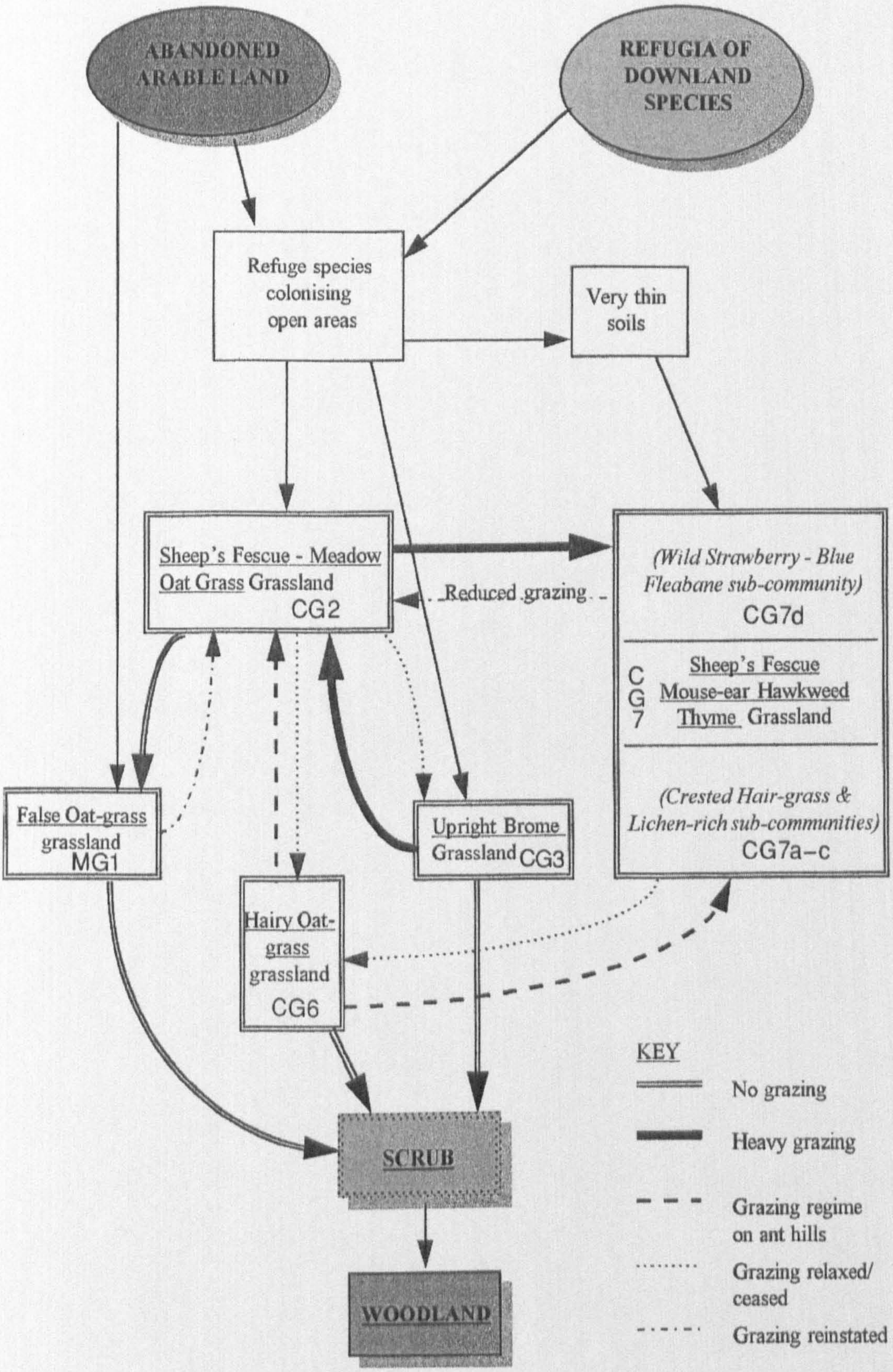
The DECORANA ordination for the Porton 1997 data produced similar results to that of 1995 and is shown in Figure 3.2. The mesotrophic grassland (MG1/5) complex is again well separated from the calcareous grassland groups. Within the latter group, the CG2 and CG7 types show a similar degree of overlap as in the 1995 ordination and both occupy the left side of the ordination space. The main differences are shown by the calcareous grassland types CG3 and CG6. CG6 is known to occur on more mesotrophic soils on flatter areas, which is why most of this NVC type has been converted to agriculture (Rodwell, 1992). This is also why the sites for this community occupy the centre (as in the 1995 analysis) and the mesotrophic end of the ordination. The high degree of overlap of the CG3 community with CG2 and CG7 probably reflects the increasing level of rabbit grazing during the mid to late 1990s at Porton. Environmental Change Network monitoring data from spotlight counts showed an increase in the rabbit 'head' count index (Bealey *et al* 1999) from 135 to 513 between 1995 and 1997, an increase of 380 per cent.

Grazing of the highly palatable *Bromus erectus* has suppressed its dominance in the sward and probably reduced the frequency of the associates which distinguish the community.

A model of vegetation dynamics at Porton Down was developed (Bealey 1999) partly from earlier models of Wells (1976) for Porton Down and Jones-Walters (1990) for Aston Rowant and Martin Down and partly from the above analyses and is shown in Figure 3.5. It clearly shows the tendency for CG3 communities to move towards CG2 under heavy rabbit grazing and the dynamic relationship between CG2 and CG7 communities, both of which are reflected in the Porton Down DECORANA ordinations.

The DECORANA ordination site plots for axis 1 and 2 for the Fragmented Site 1996 transect data is shown in Figure 3.3. This ordination plot reveals a much closer relationship between the CG grasslands and the MG1/5 groups. The CG2 complex is fairly distinct but there is a large degree of overlap between the CG3/CG6 groups and MG1/5. This probably reflects the within-site complexity of communities on the less well-grazed sites. Here, habitat mosaics occur over relatively short distances, whereas the grazed sites tend to be equally grazed all over (and therefore show uniformity among the CG2 group). Axis 1 is clearly an axis reflecting grazing management intensity, going from well grazed on the left to ungrazed, with developing scrub, to the right. The position of the species-poor MG6 group at the top of the ordination reflects improved grasslands. Only one transect was classified as CG7. This reflects the true rarity of this type in southern Britain outside Porton Down (Rodwell 1992).

Figure 3.5: A model of vegetation dynamics at Porton Down



3.3 RABBIT INDICES

The relationship between sward height and two measures of fecal pellet production at two sample nests is shown in Table 3.2. The relationship generally increases in strength from the less than 8 day measure in $1m^2$ to the total number of pellets in $4m^2$.

Table 3.2: Spearman rank correlation coefficients between sward height and fecal pellet production measures

	Quadrat size	
	$1m^2$	$4m^2$
Fecal pellets <8 days	-0.491***	-0.524***
Total No. fecal pellets	-0.513***	-0.512***

*** All significant at $P < 0.001$.

It was felt safe to conclude that a simple measure of total number of fecal pellets in the $4m^2$ sample would be an accurate estimate of rabbit grazing intensity for this study.

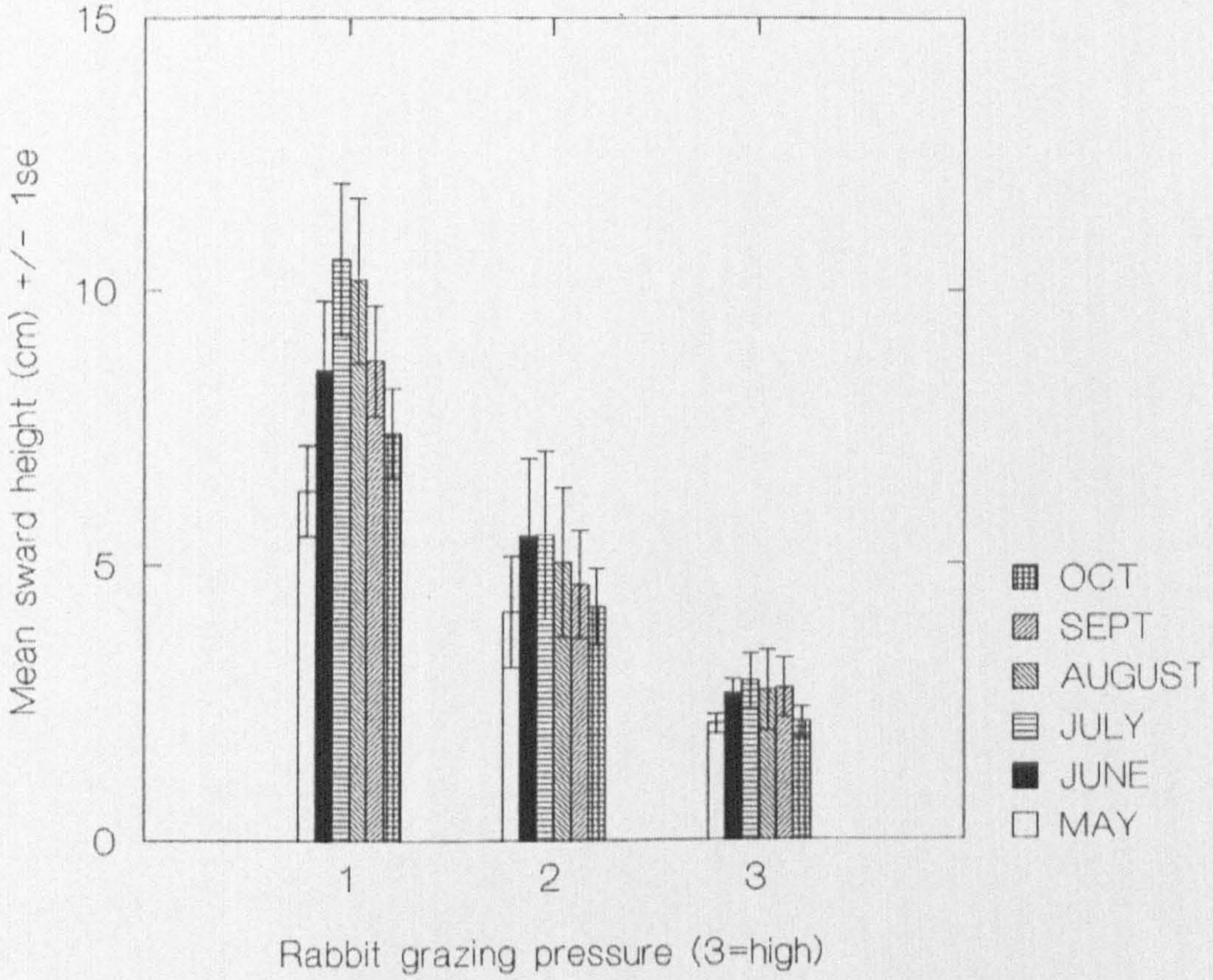
To ensure that this measure related to that used by Dolman & Sutherland (1992 – see Section 2.8.1), twenty permanently marked $4m^2$ quadrats were randomly selected from a series of fifty two used for vegetation monitoring by the ECN project at Porton Down and were re-located in June and July 1998. Total fecal pellet counts were carried out in these quadrats and then all fecal pellets were removed. After a period of between 14 and 20

days, quadrats were re-visited and the number of fecal pellets were counted. This gave a daily rate of fecal pellet production for each quadrat. The relationship between this rate (Ln transformed) and total pellet count was significant ($F_{1,18} = 4.459$; $P = 0.049$). The measures are therefore complimentary.

3.4 SWARD HEIGHT ASSESSMENTS

Figure 3.6 shows the average sward heights grouped by rabbit grazing pressure and for each sample period. It is clear that overall sward heights at any season are strongly influenced by grazing pressure. Also, sward heights follow a curve where initially, biomass growth is greater than that consumed by rabbits. By July, an equilibrium is reached and thereafter grazing reduces biomass and also height quite rapidly. The heavily grazed (rank = 3) sward only varies by a centimetre or so on average over the whole season and some of this is due to flowering spikes of species such as *Sanguisorba minor* in mid-summer. The effect shown by the least grazed (rank = 1) group is augmented by the death and physical collapse of tall grass tussocks in totally ungrazed areas.

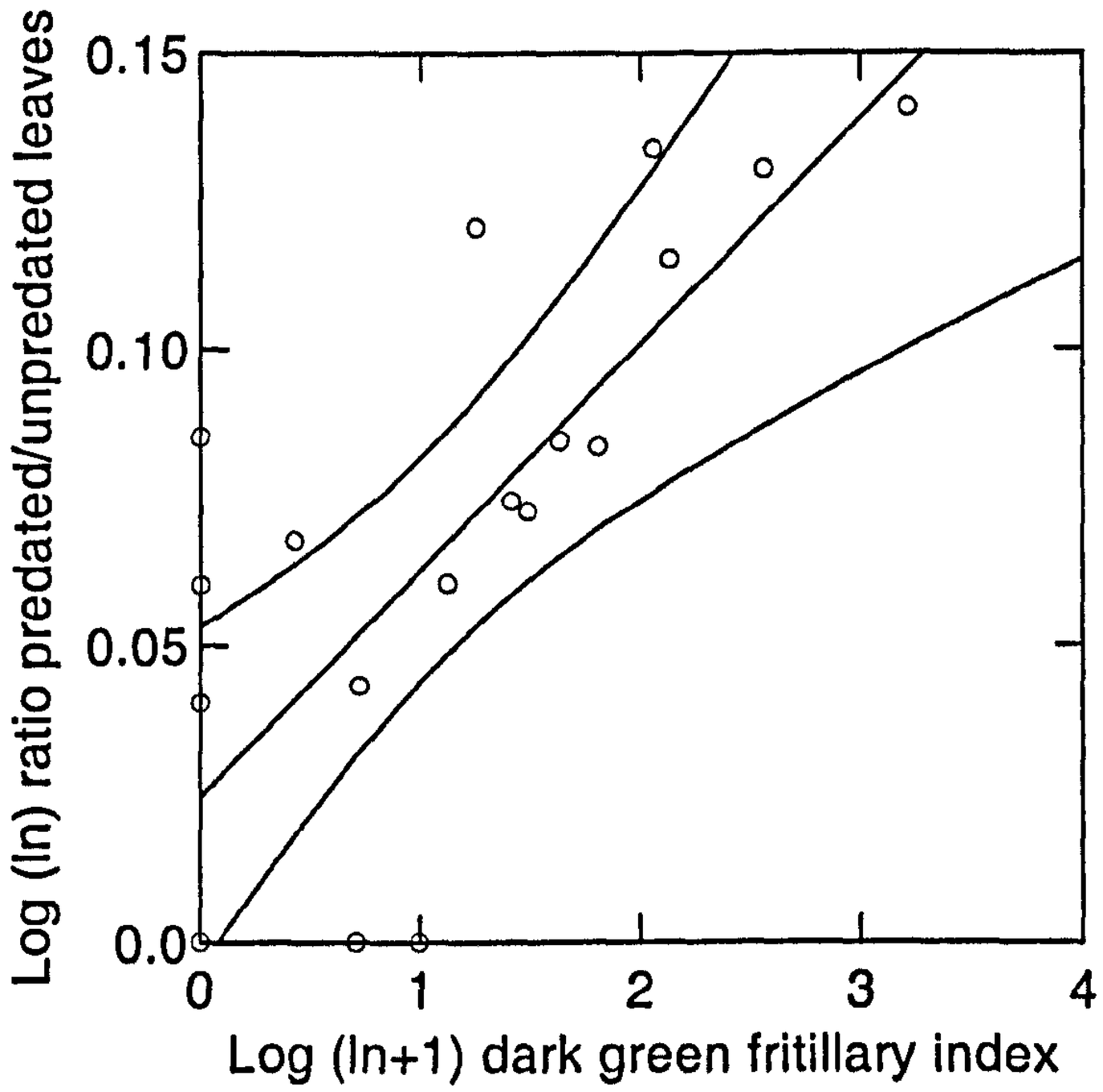
Figure 3.6: Average sward heights grouped by rabbit grazing pressure for each sample period



3.5 ADULT VERSUS LARVAL POPULATIONS

Figure 3.7 shows the relationship between adjusted adult counts and larval food-plant predation rate of dark green fritillary on a log-log scale for 1997. This relationship is highly significant ($F_{1,18} = 25.594$; $P << 0.001$).

Figure 3.7: The relationship between adjusted adult counts and larval food-plant predation rate of dark green fritillary in1997 (95 per cent confidence limits shown)



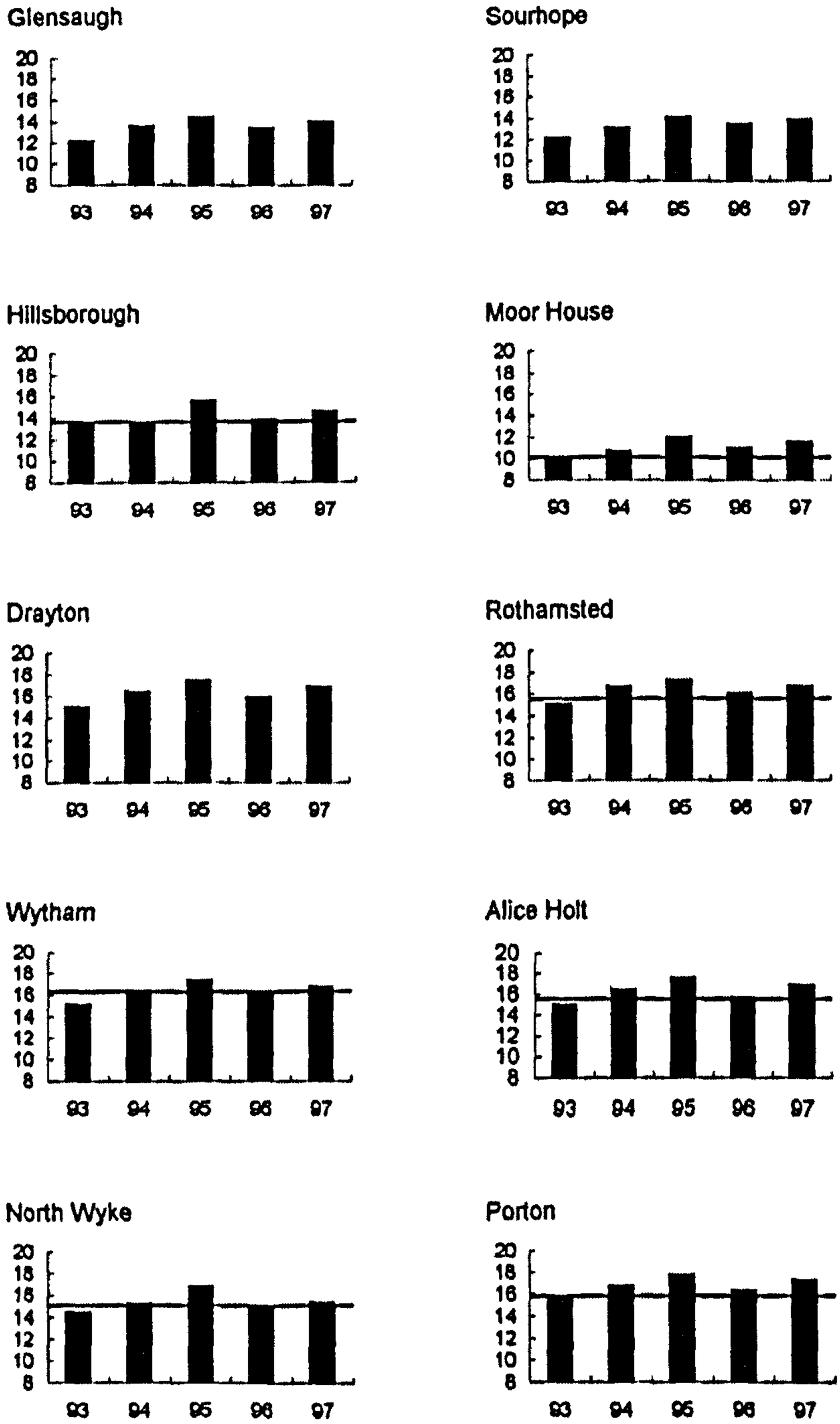
Dark green fritillaries are strong fliers and would find it easy to travel many hundreds of metres and further, to find suitable habitat for resource requirements other than that associated with breeding. It would seem reasonable to assume from this study therefore, that counts and indices based on adult numbers are a good index of habitat use over the entire butterfly species life-cycle for most if not all species in this study.

3.6 THE 1995 SUMMER DROUGHT

The summer of 1995 was one of the warmest and driest in the UK since records began. June - August rainfall was the lowest in the 229 year combined series for England and Wales, while temperatures in August 1995 were the second highest for any month in the 336 year Central England Temperature Record (Marsh 1996). Most of 1996 also had below average rainfall and some aspects of the drought, such as dry soil conditions, persisted until 1997, despite some wet periods in autumn 1995 and winter 1995-96 (Morecroft *et al* 2000). June – August means for temperature and rainfall at all terrestrial ECN sites between 1993 and 1997 are shown in Figures 3.8a & b.

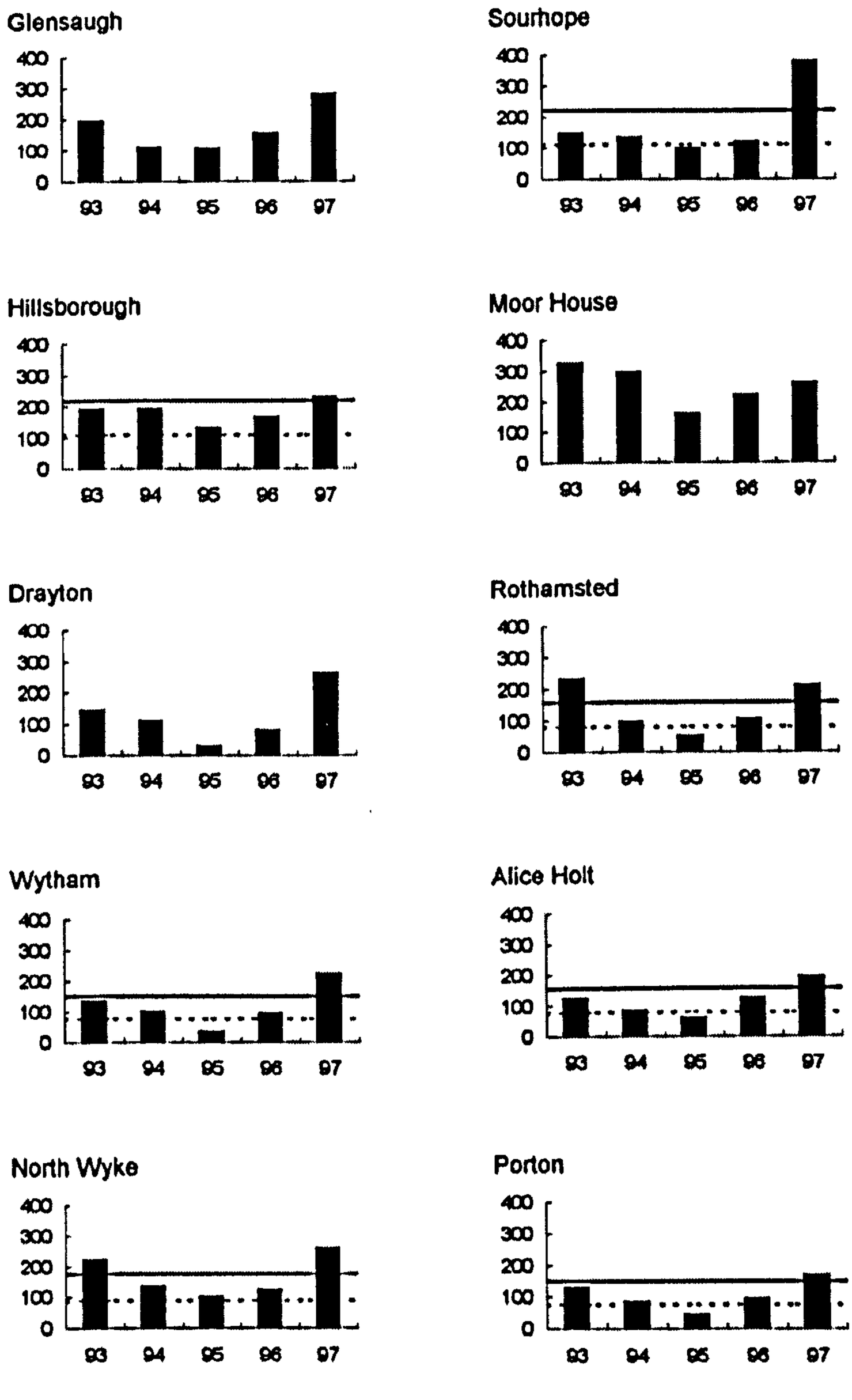
It can be seen from these figures that Porton Down experienced extreme drought and high temperatures. The general effects of this drought are being investigated across the ECN for butterflies and other invertebrate groups (Morecroft *et al* In Press). It is clear that, in considering data from this period, particular care must be taken to account for unusual behaviour in the day-flying butterflies. This is particularly the case for species which may have been searching for less desiccated food-plants on which to lay their eggs. Such plants may have been situated in more sheltered areas or even different habitats and microhabitats compared to more 'normal' years (Dennis 1993).

Figure 3.8a: June – August means for temperature at all terrestrial ECN sites between 1993 and 1997



Footnote: 1985-1995 mean values shown by horizontal line

Figure 3.8b: June – August means for rainfall at all terrestrial ECN sites between 1993 and 1997



Footnote: 1985-1995 mean values shown by horizontal line. 50 per cent of mean (drought) shown by dashed line.

3.7 DISCUSSION

As a prelude to investigations into butterfly-habitat relationships, this chapter has proven useful in setting out the context in terms of vegetation dynamics and relationships among calcareous grassland communities. Relationships between soil type, grassland age, management and calcareous grassland communities will clearly influence butterfly species and communities in terms of food-plant abundance and other preferred habitat features.

4. REGRESSION ANALYSIS OF BUTTERFLIES ON PORTON DOWN

4.1 INTRODUCTION

This chapter presents analyses of butterfly presence or population density (for the commonest species) as defined by habitat and environmental variables and therefore defines species' baseline models at the local scale. Analyses are presented by taxonomic order given in Thomas and Lewington (1991).

4.2 OVERVIEW OF ANALYSIS OF SMALL SKIPPER *Thymelicus sylvestris* AND ESSEX SKIPPER *Thymelicus lineola*

There was an initial problem in the use of data gathered in the field in that, due to field identification difficulties, small and Essex skippers were sometimes recorded as 'small' skipper species where identification was not possible down to species level. Some sample transects may have had records of Essex plus 'small', small plus 'small', all three or only 'small'. It was decided that where one true species was recorded plus 'small' then the sample could not be used for analysis for the alternative true species, as there is no way of knowing the probability of the alternative true species being present. Also, where only 'small' skippers were recorded in a transect, that sample would not be used for analysis for either species. This should not have biased the analyses as identification to true species was usually weather dependant, with specific identification more likely during cooler weather as the butterflies were less active.

4.3 SMALL SKIPPER *Thymelicus sylvestris*

Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-7.988 (2.604)		
MG5/6	-11.46 (34.49)	5.168	0.02301
Food-plant	1.131 (0.4957)	9.03	0.002656
Bare*Sward	0.07278 (0.03592)	6.926	0.008495

(Total Model Scaled Deviance $\chi^2_3 = 20.8$; $P < 0.001$)

It was not possible to test the predictive power of this model against 1997 Porton Down data as small skippers were very scarce in this year (frequency of 3 out of 55 transects where data were useable for this species, see Section 4.2). To test the predictive power of the model, predicted P-values were therefore calculated for the 1996 Fragmented Site data and regressed against Fragmented Site transect count totals. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.166$; $n = 71$, $P > 0.1$).

This model was however generated from a small sample size (frequency of presence = 9 out of 50 transects in 1995), which may explain its lack of predictive power.

Analysis of Fragmented Site local scale data revealed an apparently better model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	3.28 (0.9363)		
Rabbit Index	-0.1991 (0.08802)	12.43	<0.001
Bare	-0.7761 (0.2161)	20.15	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 29.88$; $P << 0.001$)

To test the predictive power of the model, predicted P-values were calculated for the 1995 Porton Down data and are shown plotted against transect count totals in Figure 4.1. This relationship approaches significance (Spearman Rank Correlation Coefficient, $r_s = 0.268$; $n = 50$, $P > 0.05$).

4.4 ESSEX SKIPPER *Thymelicus lineola*

Analysis of the 1995 Porton Down data produced a poor model with very large variable coefficients. This model was:

Logit (-55.95 -(0.2148*Rabbit Index)-(47.04*CG6)-(3.366*Aspect)+(6.349*Nectar Sources)+(1.478*(Bare*Sward Height))

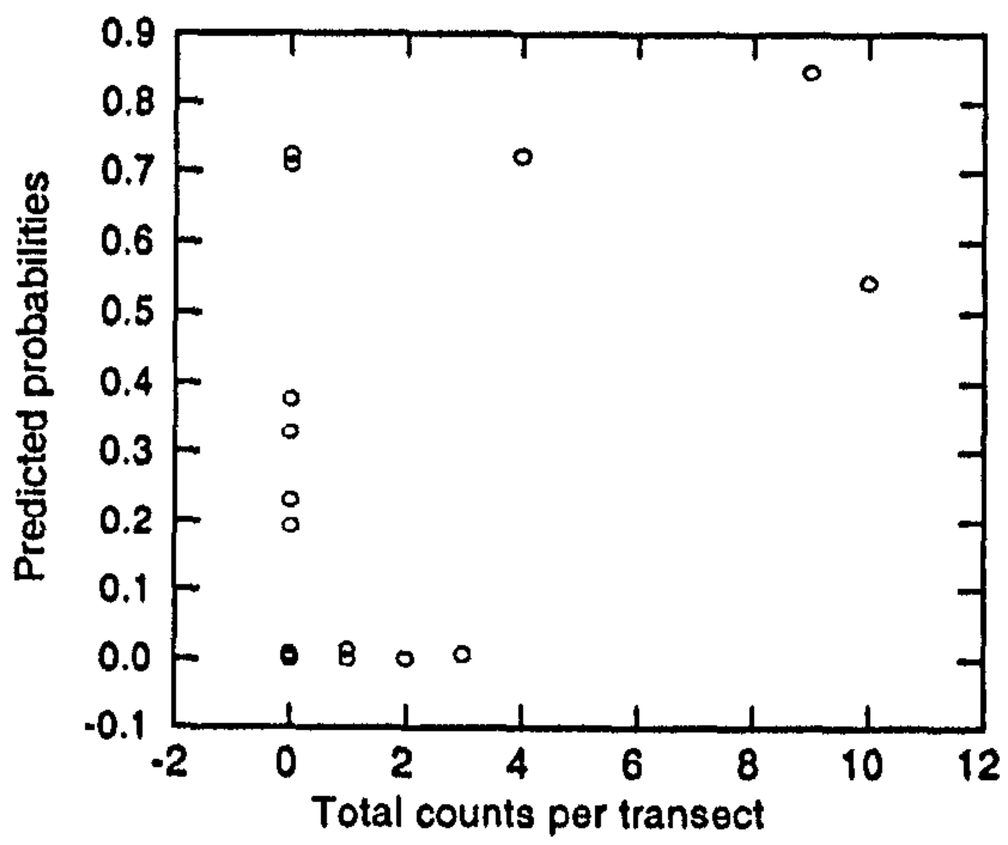
Modelling iteration was stopped as there was no further convergence. This was due to the small sample size (frequency of presence = 8 out of 49 transects under the above criteria).

Analysis of Fragmented Site local scale data revealed an apparently better model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-0.2891 (0.8829)		
Rabbit Index	-0.3588 (0.1493)	18.3	<0.001
Scrub	0.4355 (0.173)	8.467	0.003612
Bare*Stones	-0.1292 (0.03837)	17.3	<0.001

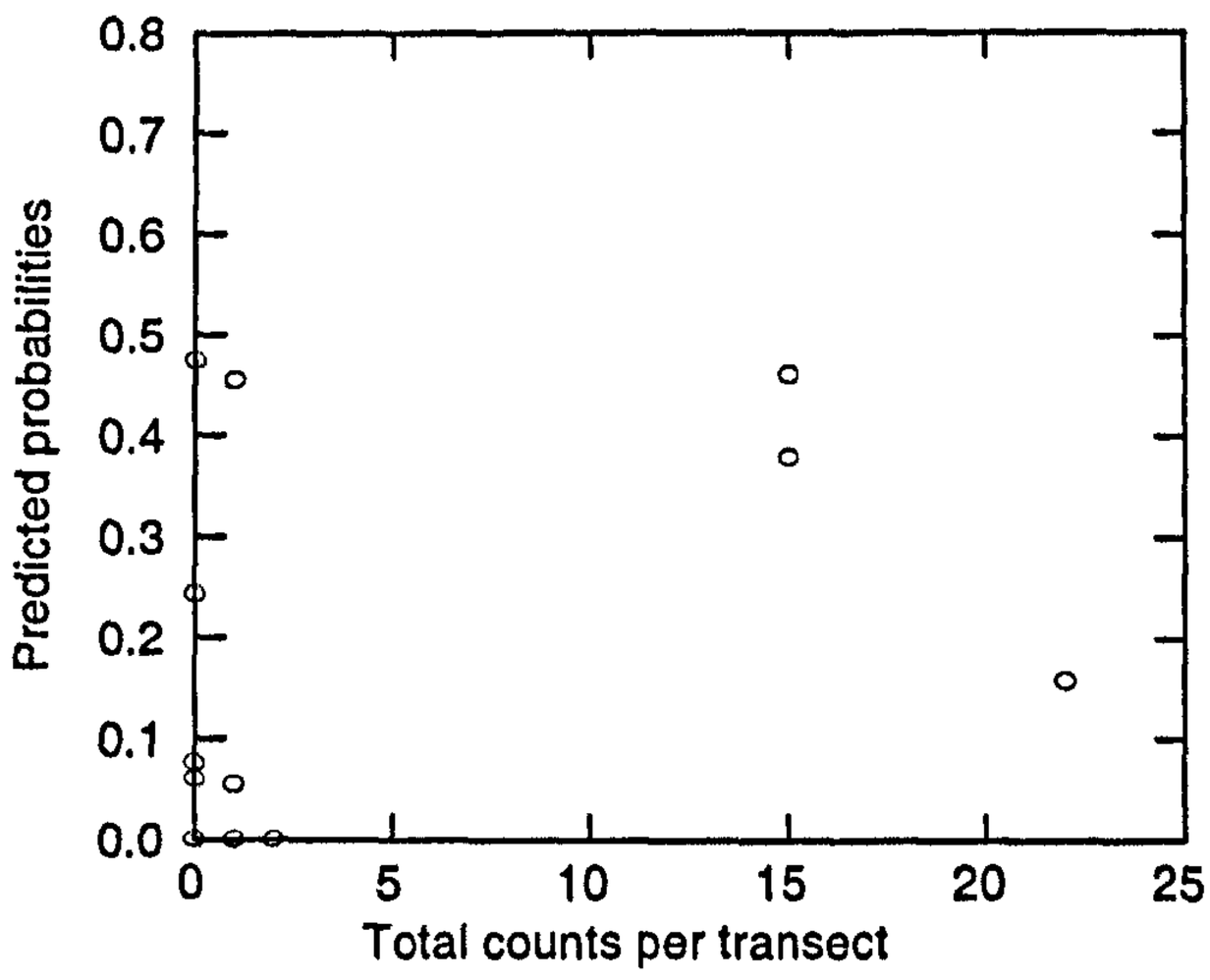
(Total Model Scaled Deviance $\chi^2_3 = 39.36$; $P << 0.001$)

Figure 4.1: The relationship between predicted P-values generated from 1995 Porton Down data and transect count totals for small skipper



To test the predictive power of the model, predicted P-values were calculated for the 1995 Porton Down data and are shown plotted against transect count totals in Figure 4.2. This relationship is highly significant (Spearman Rank Correlation Coefficient, $r_s = 0.444$; $n = 47$, $P < 0.002$).

Figure 4.2: The relationship between predicted P-values generated from 1995 Porton Down data and transect count totals for Essex skipper



4.5 SUMMARY OF SMALL AND ESSEX SKIPPER MODELS

It would seem that models generated from Fragmented Site local scale data have medium to strong predictive power when applied to Porton Down data. They are therefore considered adequate for predictive and descriptive use on a regional basis and between years.

4.6 SILVER-SPOTTED SKIPPER *Hesperia comma*

Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-2.09 (0.696)		
MG1	-9.306 (20.94)	9.701	0.001842
Slope	0.4975 (0.1659)	16.74	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 26.45$; $P < 0.001$)

When the 1995 model was used to generate P-values from 1997 Porton Down data and then regressed against total counts on the same transects, there was no relationship (Spearman Rank Correlation Coefficient, $r_s = -0.051$; $n = 67$, NS).

The conventional wisdom is that in the UK, the silver-spotted skipper selects south-facing slopes where it can warm up in direct sunlight and it can lay eggs on small tussocks of sheep's fescue *Festuca ovina* on the edges of bare ground. This allows eggs and early larval instars to develop in an environment where temperatures are raised above the surrounding ambient (BUTT 1986; Thomas *et al* 1986). During the 1995 summer flight-period, conditions became very hot and dry (see Section 3.6) and much of the grassland became desiccated. Lepidopterists at other sites reported seeing silver-spotted skippers in cooler habitats where they had never been seen before.

A plot of log-transformed (ln) mean counts grouped by aspect (Figure 4.3) reveals that silver-spotted skippers were actively seeking cooler aspects, or were actively avoiding hot and dry aspects during their 1995 flight-period. Comparison with the 'availability' of aspect on the sample transects reveals that this is definitely the case (Figure 4.4).

The same plots for transects sampled in 1997 on Porton Down (Figures 4.5 and 4.6) shows that in that year, silver-spotted skippers were selecting by aspect in a much more expected fashion. The summer of 1997, although temperatures were almost as high as those recorded in summer 1995, did not experience drought conditions (see Section 3.6). It is reasonable therefore, to assume that this species was selecting habitat using criteria observed during the majority of 'normal' years in terms of weather during 1997.

Figure 4.3: Log-transformed (ln) mean counts grouped by (median) aspect for silver-spotted skipper in 1995

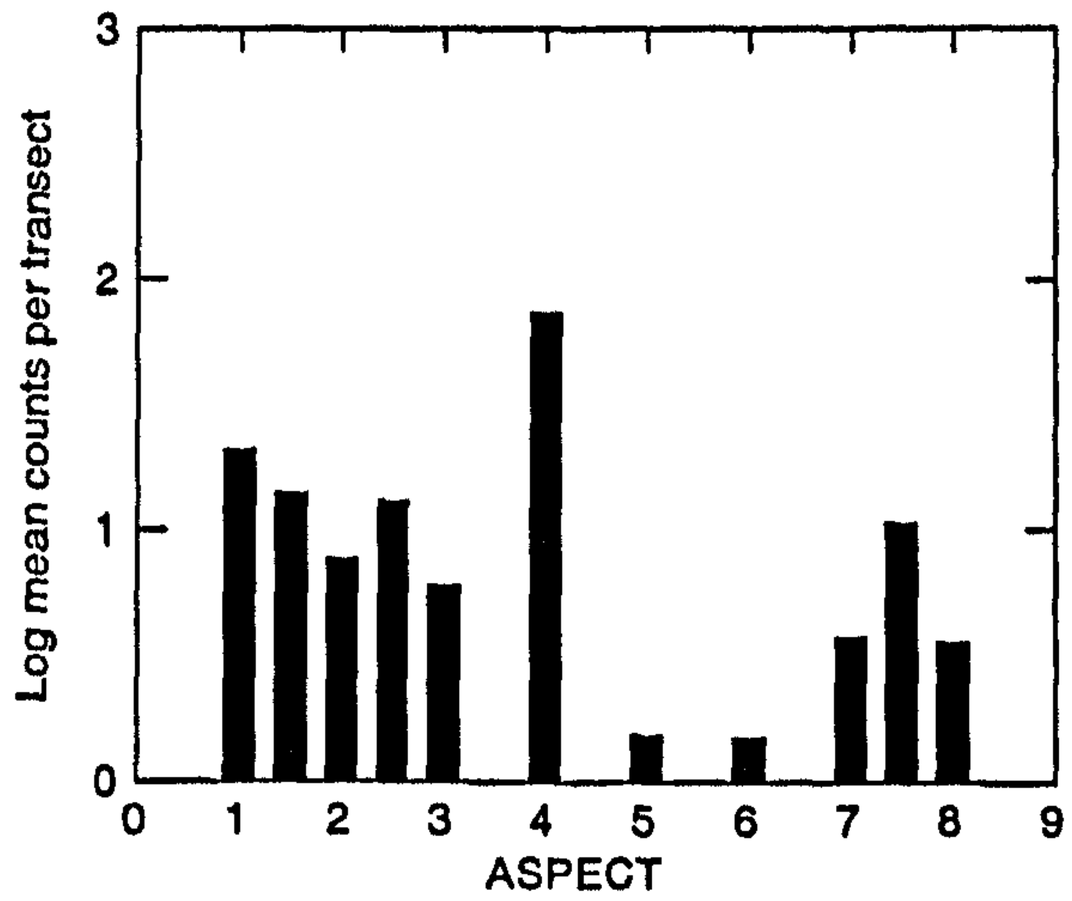


Figure 4.4: Availability of aspect to silver-spotted skippers on the sample transects in 1995

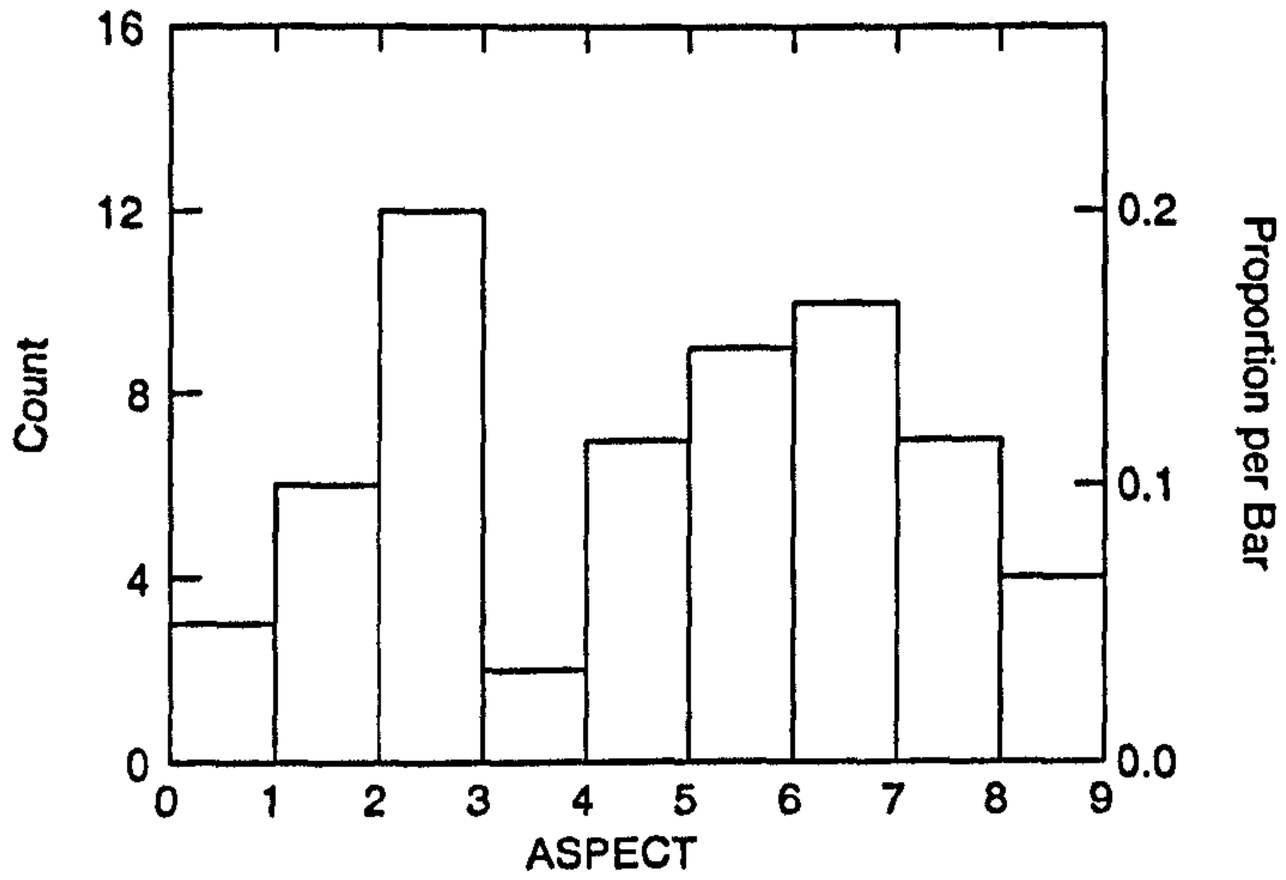


Figure 4.5: Log-transformed (ln) mean counts grouped by (median) aspect for silver-spotted skipper in 1997

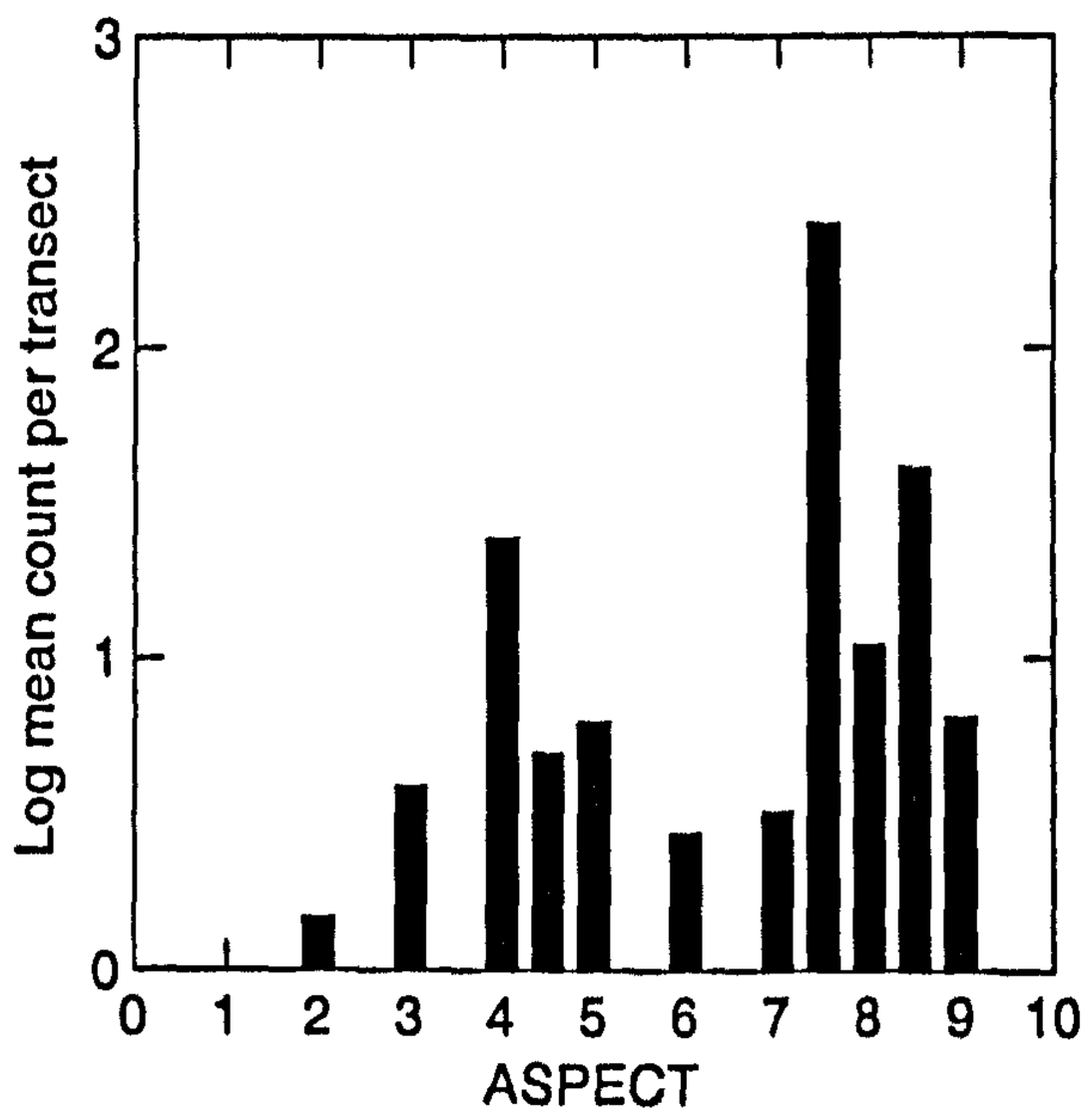
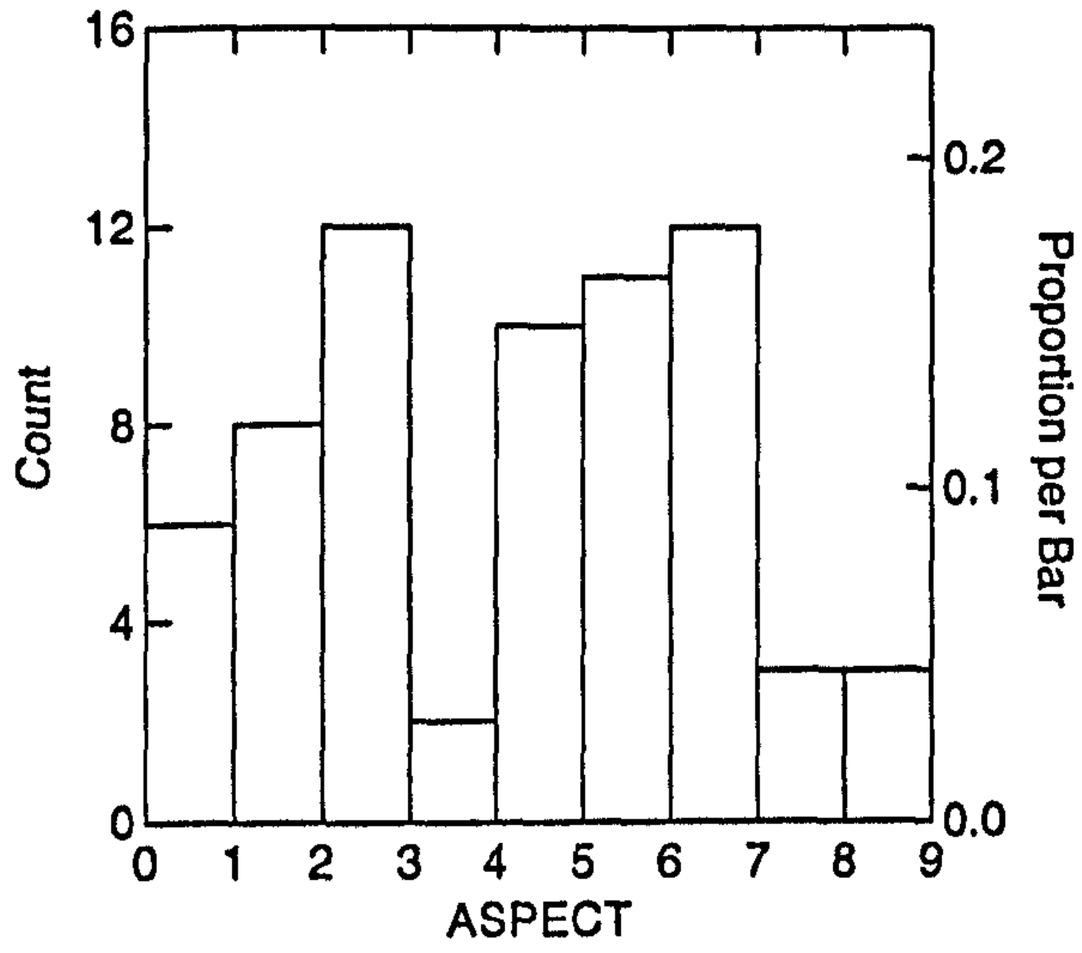


Figure 4.6: Availability of aspect to silver-spotted skippers on the sample transects in 1997



A model was therefore produced using Porton Down 1997 data. This was:

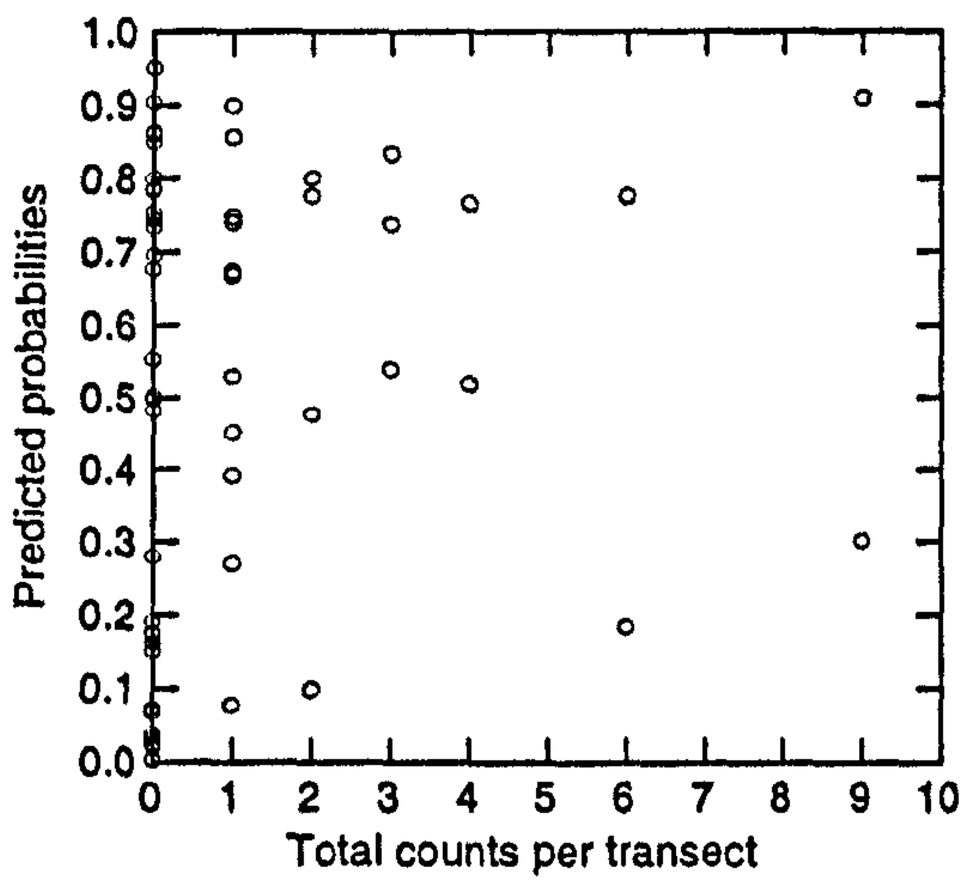
Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-5.726 (1.884)		
CG6	2.795 (1.428)	4.677	0.03057
Slope	-0.09228 (0.04935)	3.98	0.04604
Food-plant	0.5572 (0.1988)	11.85	<0.001
Nectar Sources	0.5397 (0.2083)	8.345	0.003868

(Total Model Scaled Deviance $\chi^2_4 = 26.04$; $P < 0.001$)

When predicted P-values were generated from the 1995 Porton Down data set and plotted against counts on the same transects, there was a significant relationship (Figure 4.7), (Spearman Rank Correlation Coefficient, $r_s = 0.284$; $n = 60$, $P < 0.05$).

Given the above scenario, it is reasonable to assume that this model is adequate to predict and describe silver-spotted skipper habitat selection behaviour during most 'normal' years in terms of weather, although its adequacy as a regional model is questionable.

Figure 4.7: The relationship between predicted P-values generated from 1995 Porton Down data and transect count totals for silver-spotted skipper



4.7 LARGE SKIPPER *Ochlodes venata*

Analysis of the 1995 Porton Down data produced the following model:

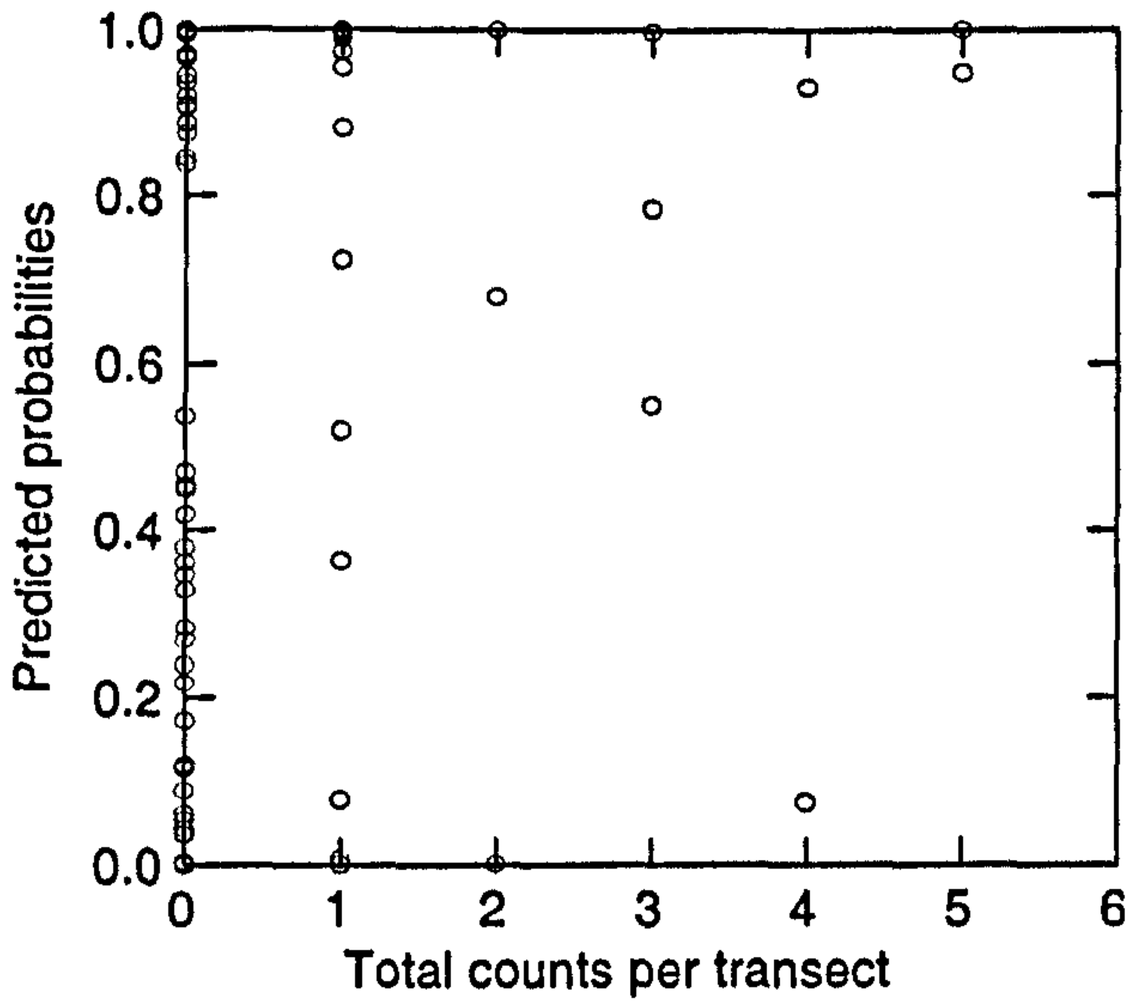
Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-3.291 (1.872)		
CG3	6.356 (2.117)	22.02	<0.001
Aspect	-1.52 (0.5424)	20.37	<0.001
Bare*Sward	0.1761 (0.07542)	11.57	<0.001
Food-plant	0.7212 (0.4014)	4.277	0.03863

(Total Model Scaled Deviance $\chi^2_4 = 39.63$; $P << 0.001$)

Unfortunately, the model could not be tested against 1997 Porton Down data as only two large skippers were recorded on two transects. Predicted P-values for 1996 Fragmented Site transects were generated from the 1995 Porton Down model and plotted against counts on the same transects. This showed a significant relationship (Figure 4.8), (Spearman Rank Correlation Coefficient, $r_s = 0.256$; $n = 94$, $P < 0.02$).

This is a relatively rare species on the Porton Down grasslands, but the model produced from the 1995 data, when it was slightly more widespread, does appear to reflect objective knowledge of the species' habitat requirements and carries a high degree of statistical significance. The model also appears to predict habitat selection on a regional basis quite well.

Figure 4.8: The relationship between predicted P-values generated from 1996 Fragmented Site data and transect count totals for large skipper



4.8 DINGY SKIPPER *Erynnis tages*

Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-5.106 (1.374)		
Aspect	0.3087 (0.1534)	4.634	0.03134
Food-plant	0.505 (0.1989)	8.904	0.002845

(Total Model Scaled Deviance $\chi^2_2 = 14.04$; $P < 0.001$)

When the model was tested by generating predicted P-values from the 1997 Porton Down data set and regressing these against counts on the same transects, there was no relationship, (Spearman Rank Correlation Coefficient, $r_s = 0.218$; $n = 67$, $P > 0.05$). This is another uncommon species at Porton Down and it may be that the low frequencies of occurrence (13 in 1995, 11 in 1997) may have affected the accuracy of the model for predictive purposes.

4.9 GRIZZLED SKIPPER *Pyrgus malvae*

Analysis of the 1995 Porton Down data produced a poor model where no variables were fitted to any degree of significance (the nearest being food-plant at change in scaled deviance $\chi^2_1 = 1.99$; $P = 0.1583$). This was almost certainly due to the small sample size (frequency of presence = 4 out of 60 transects).

In 1997, grizzled skippers were present in quite large numbers, probably due to the warm late winter/early spring weather. The BMS Index for 1997 at Porton Down was 86 compared to 22 in 1995. A model was therefore produced using Porton Down 1997 data. This was:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-1.983 (0.6084)		
CG7	2.12 (0.8868)	7.413	0.006475
Food-plant	0.3804 (0.1578)	6.66	0.00986

(Total Model Scaled Deviance $\chi^2_2 = 11.29$; P = 0.003535)

When the model was tested by generating predicted P-values from the 1995 Porton Down data set and regressing these against counts on the same transects, there was no relationship (Spearman Rank Correlation Coefficient, $r_s = 0.038$; n = 60, NS). This is an even less common species at Porton Down than dingy skipper and its generally low frequencies of occurrence would probably affect the accuracy of the model for predictive purposes during most years.

4.10 GREEN HAIRSTREAK *Callophrys rubi*

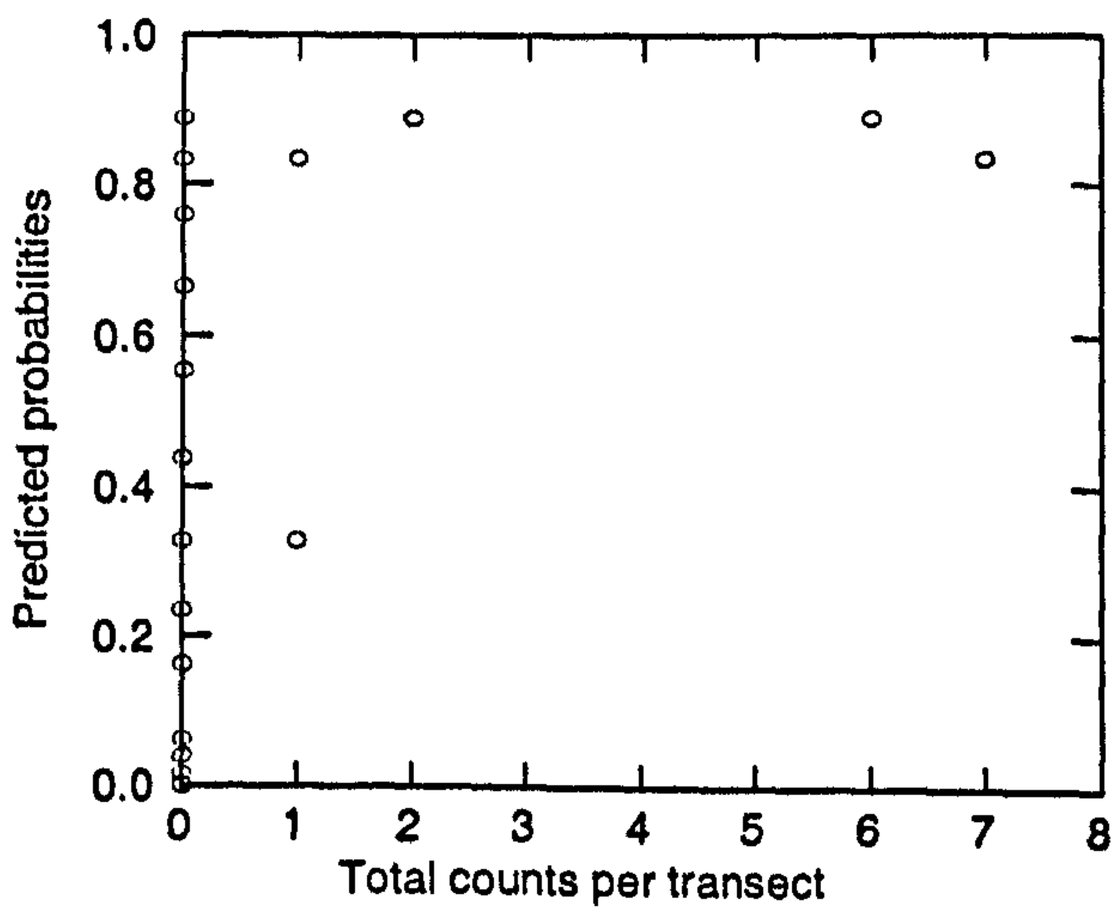
Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-4.109 (1.297)		
CG2	2.47 (1.013)	7.776	0.005294
CG6	-8.611 (15.66)	4.691	0.03032
Scrub	0.4648 (0.1452)	14.19	<0.001

(Total Model Scaled Deviance $\chi^2_3 = 27.48$; $P << 0.001$)

To test the predictive power of the model, predicted P-values were calculated for the 1997 Porton Down data and are shown plotted against transect count totals in Figure 4.9. This relationship is highly significant (Spearman Rank Correlation Coefficient, $r_s = 0.408$; $n = 67$, $P < 0.001$).

Figure 4.9: The relationship between predicted P-values generated from 1997 Porton Down data and transect count totals for green hairstreak



It would therefore seem that the above model is adequate for descriptive and predictive purposes between years.

4.11 SMALL COPPER *Lycaena phlaeas*

A model was initially produced using 1995 Porton Down data. However, there were no statistically significant terms in the model, the highest change in scaled deviance χ^2_1 value being 3.05 (P = 0.08074) for the parameter scrub. This model was therefore rejected.

Consequently, a model was produced using 1997 data, when small coppers were more abundant and widespread at Porton Down (1997 BMS Index of 152 compared to 54 in 1995).

This model was:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-7.525 (2.405)		
CG6	-8.475 (22.1)	4.917	0.02659
Nectar Sources	1.057 (0.3931)	10.79	0.00102

(Total Model Scaled Deviance χ^2_2 = 12.76; P = 0.001695)

To test the predictive power of the model, predicted P-values were calculated for the 1995 Porton Down data and regressed against transect count totals. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.088$; n = 60, NS). However, the test would suffer from a paucity of data in 1995 (frequency of 9 on 60 transects) as suggested by the small skipper analysis (Section 4.3).

It would therefore seem that the above model is probably adequate for descriptive and predictive purposes between years.

4.12 SMALL BLUE *Cupido minimus*

Analysis of the 1995 Porton Down data showed no significant terms but the closest to significance produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	0.8059 (1.7)		
Bare	-0.8543 (0.5629)	2.712	0.0996
Food-plant	-6.899 (25.08)	2.042	0.153

(Total Model Scaled Deviance $\chi^2_2 = 4.851$; P = 0.08843)

This species was only common in 1995 when the BMS Index at Porton Down was 45, having been 161 in 1994. Subsequently, an apparent decline has continued with BMS Indices of 9 and 10 in 1996 and 1997 respectively. This species has only one food-plant,

kidney vetch *Anthyllis vulneraria*, which is prone to boom and bust population cycles (Morton 1985), often germinating strongly after hot summers but being suppressed by a series of cool summers (BUTT 1986). Also, the small blue lays its eggs on the flowers where the larvae also develop, so lack of flowering produces a severe problem to this species (BUTT 1986). Kidney vetch was very common at Porton Down in 1994 but declined thereafter. The resulting low populations of small blues have not enabled testing or improvement of the above model.

It is not known, therefore, whether the above model is adequate for descriptive and predictive purposes between years.

4.13 BROWN ARGUS *Aricia agestis*

Analysis of the 1995 Porton Down data produced the following model:

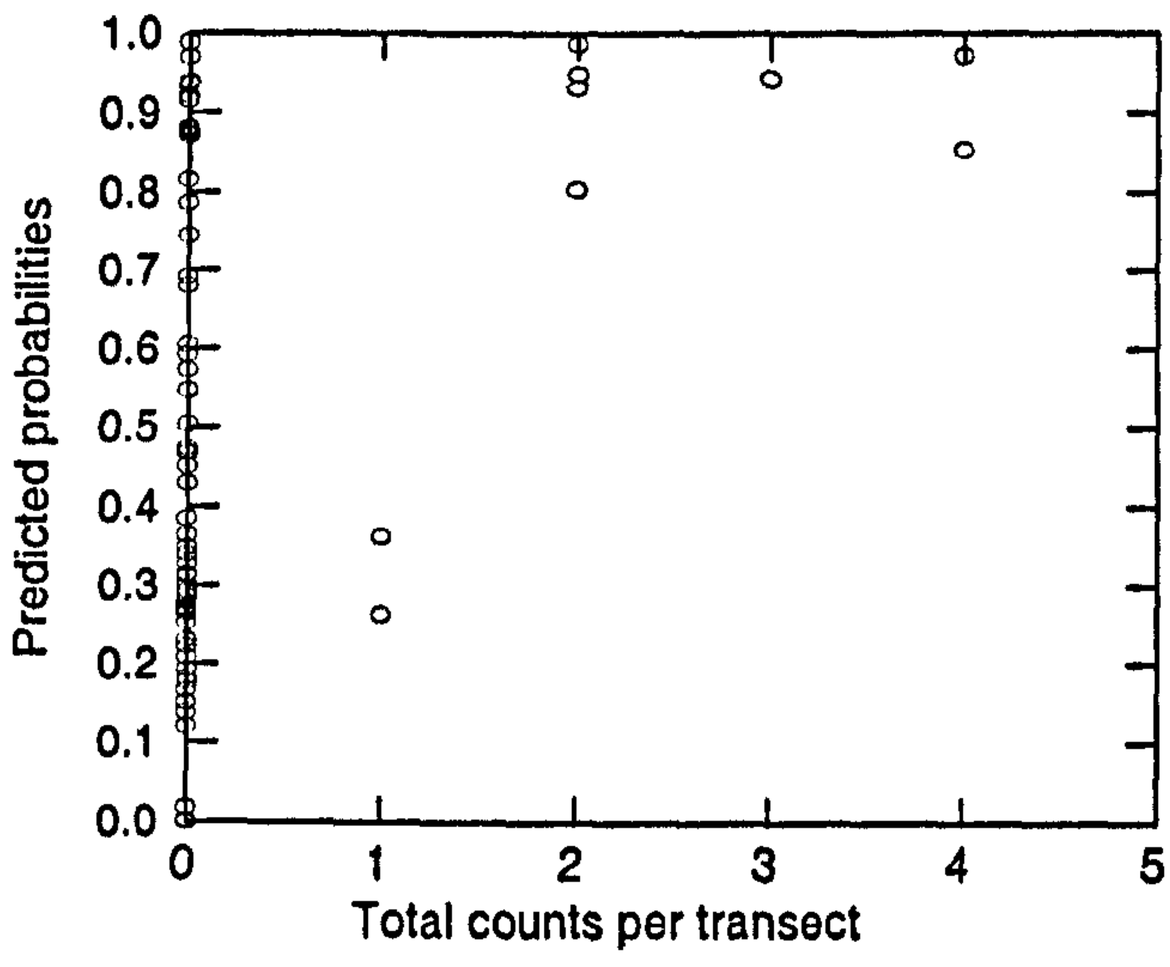
Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-0.2932 (0.9534)		
Sward Height	-0.3681 (0.1436)	10.17	0.001427
Scrub	0.3442 (0.1492)	6.339	0.01181
Food-plant	0.4259 (0.1683)	8.237	0.004104

(Total Model Scaled Deviance $\chi^2_3 = 27.32$; $P << 0.001$)

To test the predictive power of the model, predicted P-values were calculated for the 1997 Porton Down data and are shown plotted against transect count totals in Figure 4.10. This relationship is highly significant (Spearman Rank Correlation Coefficient, $r_s = 0.383$; $n = 67$, $P < 0.002$).

It would therefore seem that the above model is adequate for descriptive and predictive purposes between years.

Figure 4.10: The relationship between predicted P-values generated from 1997 Porton Down data and transect count totals for brown argus



4.14 COMMON BLUE *Polyommatus icarus*

Models were initially produced from 1995 Porton Down data using corrected indices as normal response variables. This produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,55)
Constant	2.673 (1.149)	5.415	0.02367
Sward Ht*Food-plant	0.8833 (0.01948)	20.571	<0.001
Sward Ht*Rabbit Ind.	-0.002359 (0.0007)	11.296	0.001418
Sward Ht*Bare	-0.04419 (0.02071)	4.552	0.03736
Aspect	0.2764 (0.1355)	4.16	0.0462

Scale parameter = 5.503; Filliben coefficient = 0.9926

When predicted populations were regressed against observed for 1997 Porton Down data, there was no trend and the relationship was not significant (Spearman Rank Correlation Coefficient, $r_s = -0.051$; $n = 67$, NS).

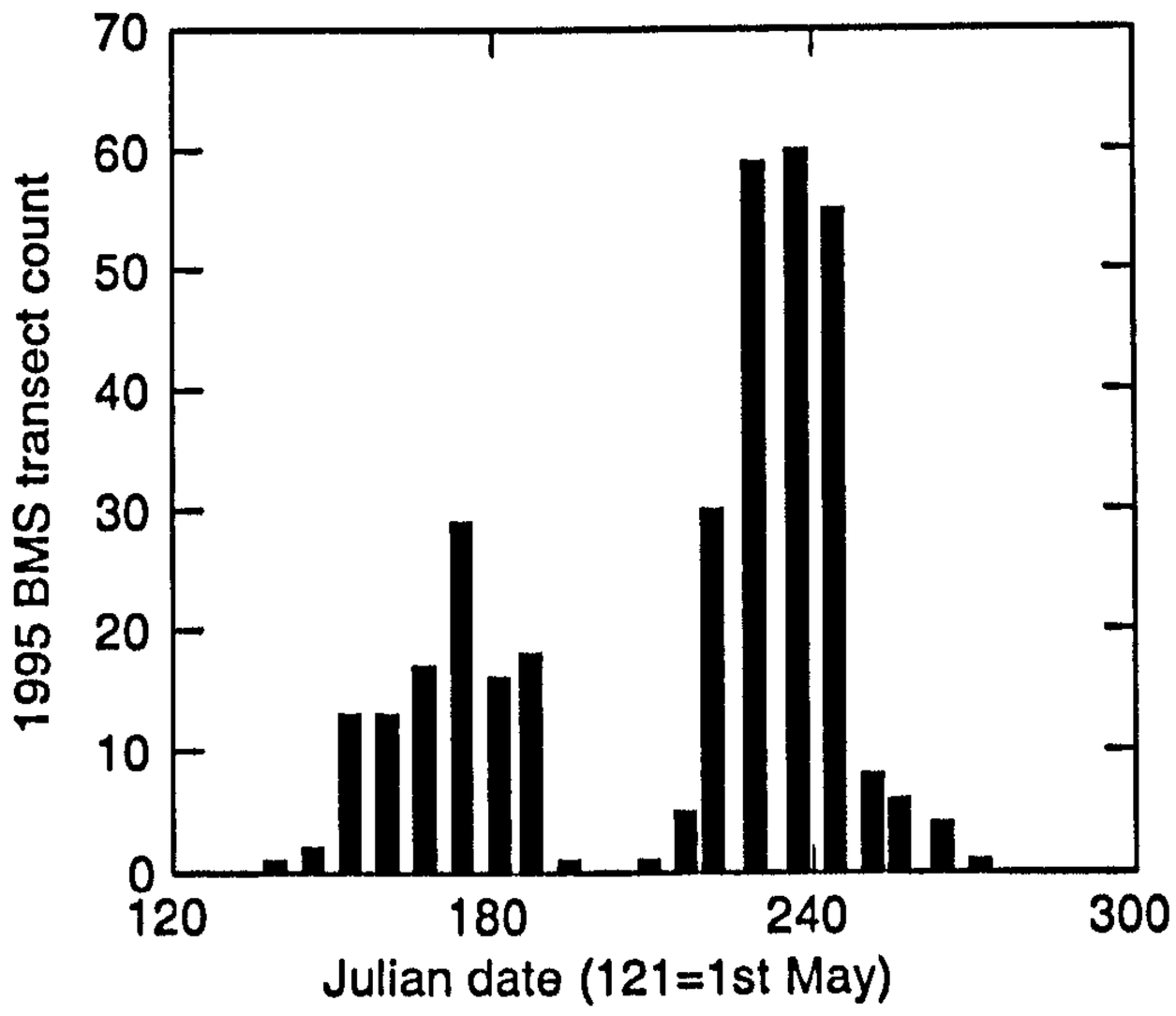
Examination of the 1995 population curve (Figure 4.11) showed that there was a very large second generation, presumably due to the increasingly warm and dry conditions prevailing during the second flight period. It is very likely, therefore, that common blue behaviour in terms of habitat selection, was atypical during this period and may have been instrumental in producing a 'false' model as with the silver-spotted skipper.

A model was therefore produced using the 1997 Porton Down data set. This model was:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,64)
Constant	2.782 (0.469)	35.177	<0.001
Slope	-0.1348 (0.03493)	14.898	<0.001
Scrub	0.185 (0.08331)	4.934	0.02988

Scale parameter = 3.326; Filliben coefficient = 0.9891

Figure 4.11: The 1995 population curve for common blue at Porton Down



Predicted populations were generated from this model for 1995 Porton Down data and regressed against (adjusted) observed. Although the relationship is a much better one than the previous it is still not significant (Spearman Rank Correlation Coefficient, $r_s = 0.226$; n = 60, $P > 0.05$).

It was decided to look at a model produced from Fragmented Site data to see whether there was any predictive power shared between models. Using individual Fragmented Site transects as independent samples, the model was: 3.648+(0.2625*Aspect); scale parameter = 14.68; Filliben coefficient = 0.974. None of the terms were significant.

This model was therefore not useable for predictive purposes.

When predicted populations for Fragmented Site 1996 data are generated from the 1995 Porton Down model and plotted against observed (Figure 4.12), this relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.243$; $n = 94$, $P < 0.02$).

It would seem that the best overall model for descriptive and predictive purposes between years and on a regional scale was the model derived from the Porton Down 1995 data.

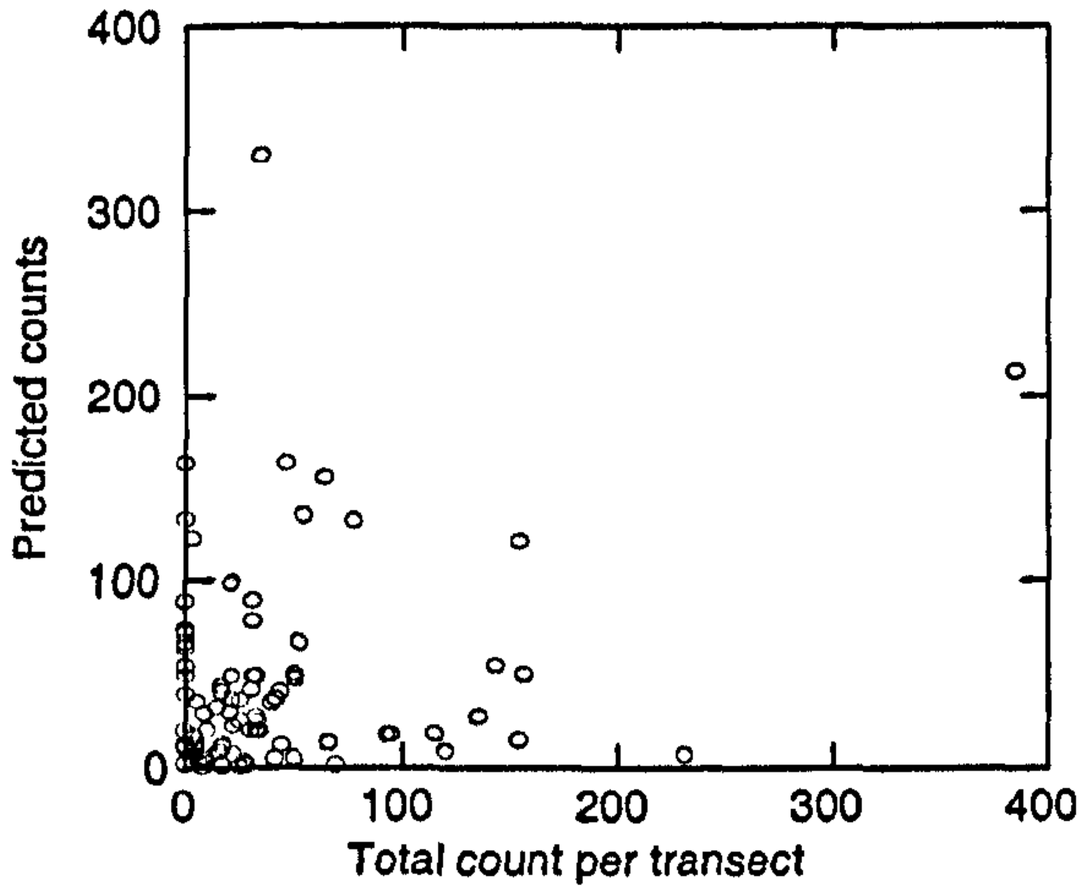
4.15 CHALKHILL BLUE *Lysandra coridon*

Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-1.122 (0.3077)		
Food-plant	4.468 (10.6)	7.976	0.00474

(Total Model Scaled Deviance $\chi^2_1 = 7.976$; $P = 0.00474$)

Figure 4.12: The relationship between predicted populations for Fragmented Site 1996 data and transect count totals for common blue



There were not enough counts from the Porton Down 1997 data to test the predictive power of this model. However, it was felt that due to the relative scarcity of the food-plant horse-shoe vetch *Hippocrepis comosa* at Porton Down, this model may not be adequate for regional and between year predictive purposes. To test this, a model was produced using Fragmented Site data. This was:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-1.592 (0.3158)		
Food-plant	0.7296 (0.1709)	26.7	<0.001

(Total Model Scaled Deviance $\chi^2_1 = 26.7$; $P < 0.001$)

Predicted P-values were generated from this model for the Porton Down 1995 data and plotted against observed count totals on the same transects (Figure 4.13). This relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.344$; $n = 60$, $P < 0.01$).

Similary, when predicted P-values were generated for Fragmented Site transects from the Porton Down 1995 model data and plotted against observed count totals on the same transects (Figure 4.14), the relationship is highly significant (Spearman Rank Correlation Coefficient, $r_s = 0.599$; $n = 94$, $P << 0.001$).

Figure 4.13: The relationship between predicted P-values generated from 1995 Porton Down data and transect count totals for chalkhill blue

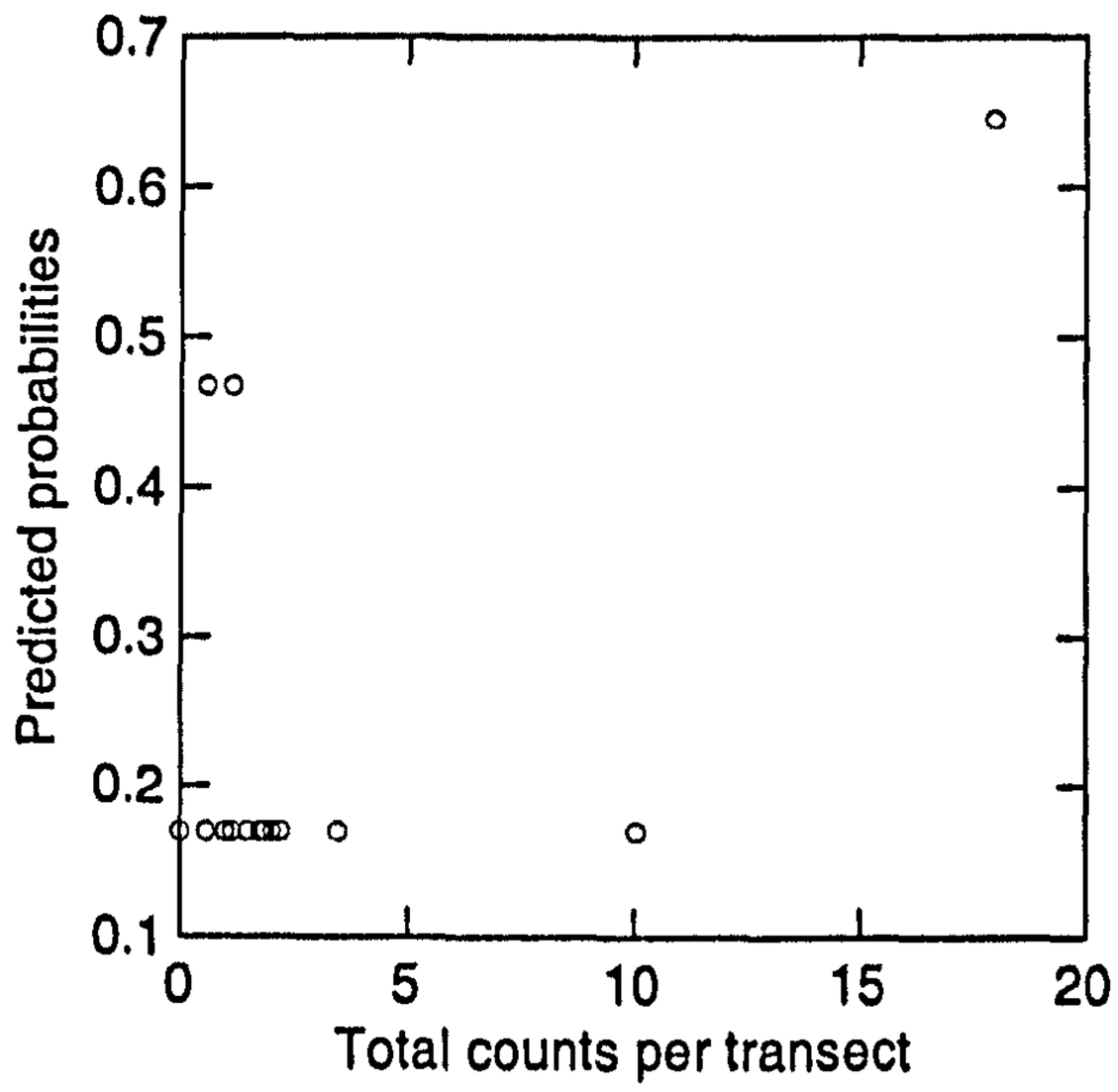
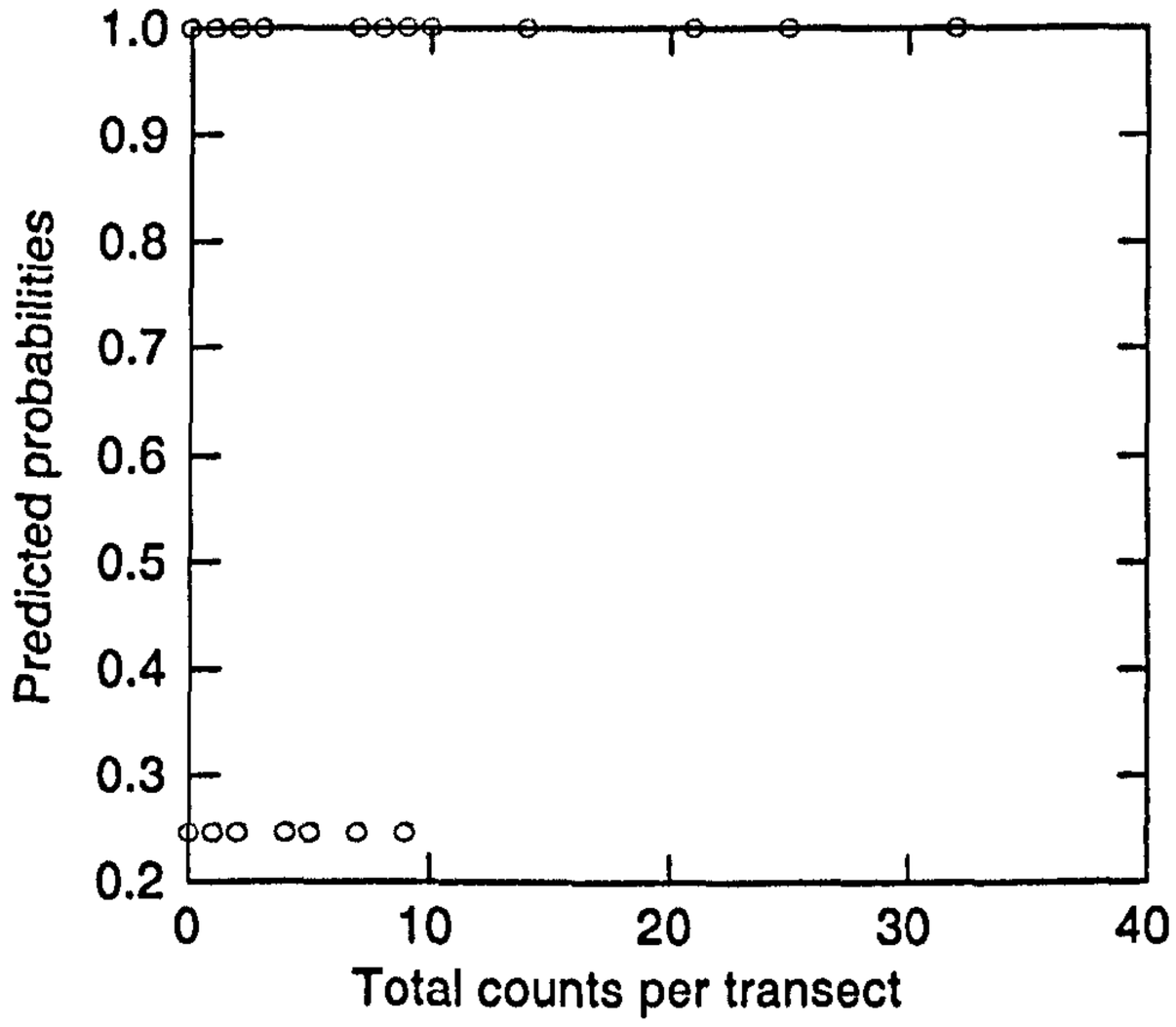


Figure 4.14: The relationship between predicted P-values generated from 1996 Fragmented Site data and transect count totals for chalkhill blue



The important feature of these models is that the food-plant is consistently selected as the single important variable at the local scale of analysis. The fact that the models vary widely in their predictive power should not be cause for concern as the food-plant coefficient would not be forced into any regional model.

4.16 ADONIS BLUE *Lysandra bellargus* and 4.17 DUKE OF BURGUNDY *Hamaeris lucina*

There were insufficient data from any year to perform modelling for these species.

4.18 DARK GREEN FRITILLARY *Argynnis aglaja*

Analysis of the 1995 Porton Down data produced the following model:

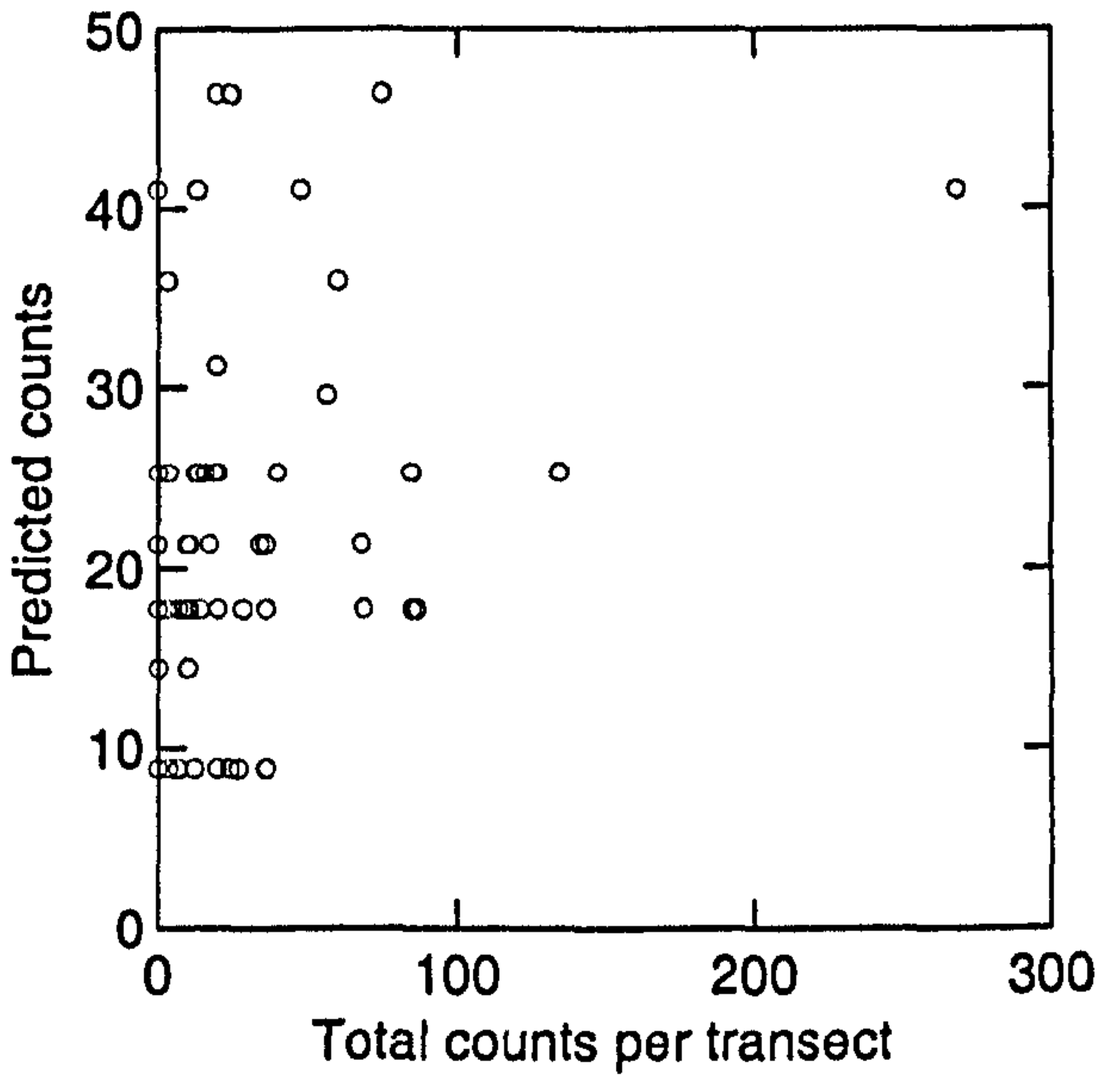
Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,55)
Constant	2.979 (0.4266)	48.77	<0.001
CG3	1.784 (0.5868)	9.239	0.003598
Food-plant	0.4101 (0.114)	12.938	<0.001

Scale parameter = 3.537; Filliben coefficient = 0.9951

This model's predictive power was tested by generating predicted populations for the 1997 Porton Down data and plotting them against observed (adjusted) populations (Figure 4.15). This relationship is highly significant (Spearman Rank Correlation Coefficient, r_s = 0.36; n = 67, P < 0.005).

This model therefore appears to be adequate to describe and predict dark green fritillary habitat selection on a between year basis.

Figure 4.15: The relationship between predicted populations for Porton Down 1997 data and transect count totals for dark green fritillary



4.19 MARSH FRITILLARY *Euphydryas aurinia* and 4.20 WALL *Lasiommata megera*

There were insufficient data from any year to perform modelling for these species.

4.21 MARBLED WHITE *Melanargia galathea*

Analysis of the 1995 Porton Down data produced the following model:

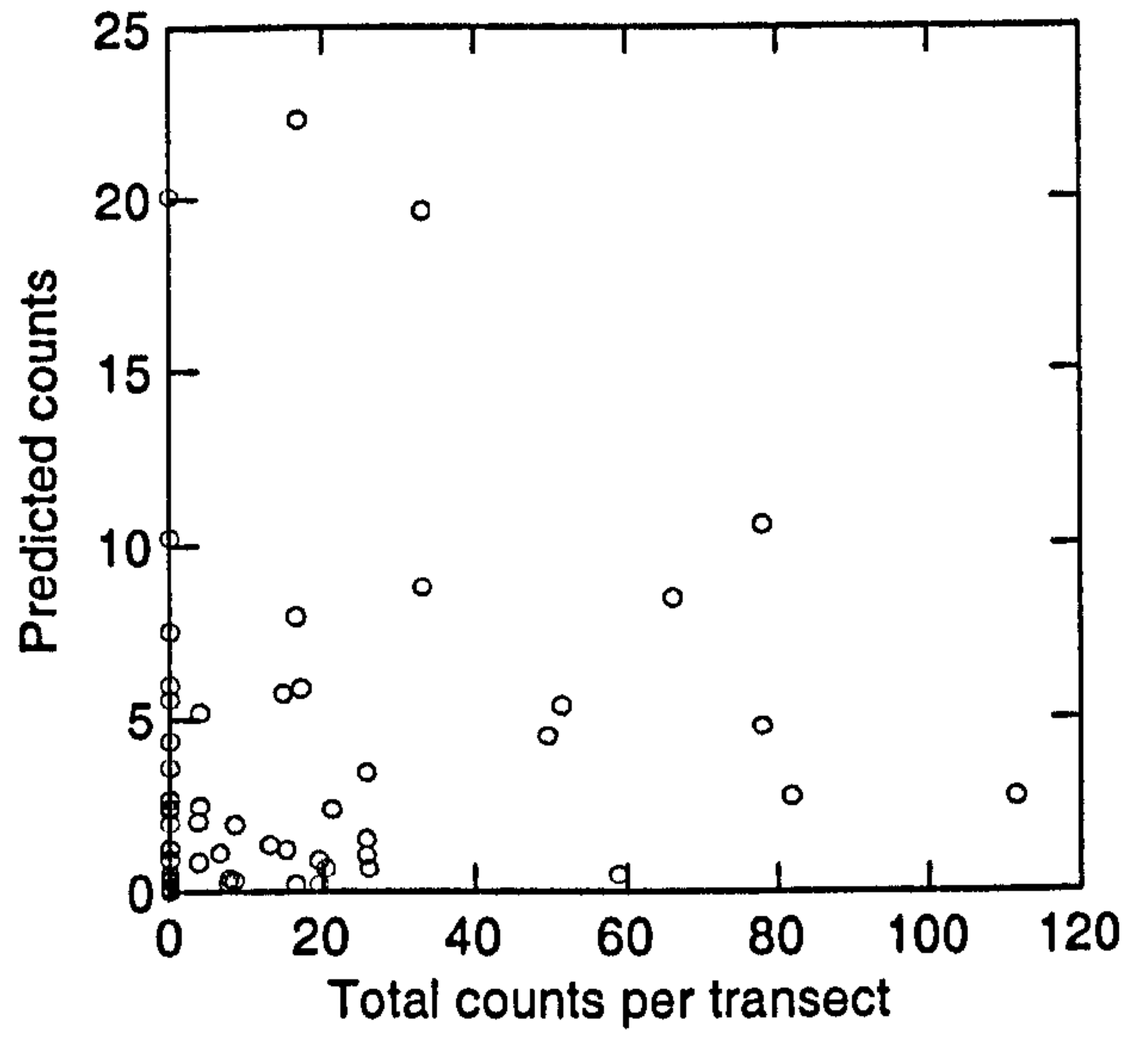
Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,55)
Constant	0.1978 (0.7378)	0.072	0.7895
Sward Height	0.2051 (0.04583)	20.023	<0.001
CG3	1.374 (0.6611)	4.32	0.04235
Scrub	0.3393 (0.09303)	13.308	<0.001
Stones	-0.5024 (0.1752)	8.218	0.005867

Scale parameter = 3.014; Filliben coefficient = 0.9952

This model's predictive power was tested by generating predicted populations for the 1997 Porton Down data and plotting them against observed (adjusted) populations (Figure 4.16). This relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.317$; $n = 67, P < 0.01$).

This model therefore appears to be adequate to describe and predict marbled white habitat selection on a between year basis.

Figure 4.16: The relationship between predicted populations for Porton Down 1997 data and transect count totals for marbled white



4.22 GRAYLING *Hipparchia semele*

There were insufficient data from any year to perform modelling for this species.

4.23 HEDGE BROWN *Pyronia tithonus*

Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	5.669 (2.357)		
Food-plant	-1.068 (0.3536)	11.94	<0.001

(Total Model Scaled Deviance $\chi^2_1 = 11.94$; $P < 0.001$)

Predicted P-values were generated from this model for the Porton Down 1997 data and regressed against observed count totals on the same transects. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = -0.086$; $n = 67$, NS).

Hedge brown is another species which is relatively rare in some years on the Porton Down grasslands (frequency of 9 on 60 transects in 1995). A model was produced using the Fragmented Site 1996 transect data to see whether it would provide stronger descriptive and predictive power. This model was:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,90)
Constant	2.274 (0.8908)	6.513	0.01239
CG3	2.197 (0.805)	7.45	0.00763
Scrub	0.3888 (0.1496)	6.752	0.01094
Rabbit Index	-0.1217 (0.04979)	5.98	0.01642

Scale parameter = 13.45; Filliben coefficient = 0.9599

This model was used to generate predicted populations for Porton Down in 1995 and 1997 and these were regressed against observed transect totals (adjusted populations were not generated due to the species' relative rarity). Neither of these show a significant relationship (Spearman Rank Correlation Coefficient, $r_s = 0.07$; n = 60, NS and $r_s = 0.061$; n = 67, NS respectively).

It would appear that neither the 1995 Porton Down nor the 1996 Fragmented Site model has a greater degree of predictive (or descriptive) power than the other. However, the 1996 Fragmented Site model possesses significant parameters that are objectively good predictors for the species and relate to current knowledge of habitat requirements (BUTT 1996) and also is based on a much larger data set from more 'typical' hedge brown habitat.

The latter model therefore appears to be generally adequate to describe and predict hedge brown habitat selection between years.

4.24 MEADOW BROWN *Maniola jurtina*

Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,53)
Constant	-0.5093 (1.521)	0.112	0.7392
MG1	-2.438 (1.044)	5.454	0.02334
Slope	0.6014 (0.1304)	21.272	<0.001
Aspect	0.564 (0.1571)	12.898	<0.001
Nectar Sources	0.812 (0.1737)	21.862	<0.001
Sward Ht*Bare	0.09533 (0.02842)	11.25	0.001476

Scale parameter = 7.122; Filliben coefficient = 0.9955

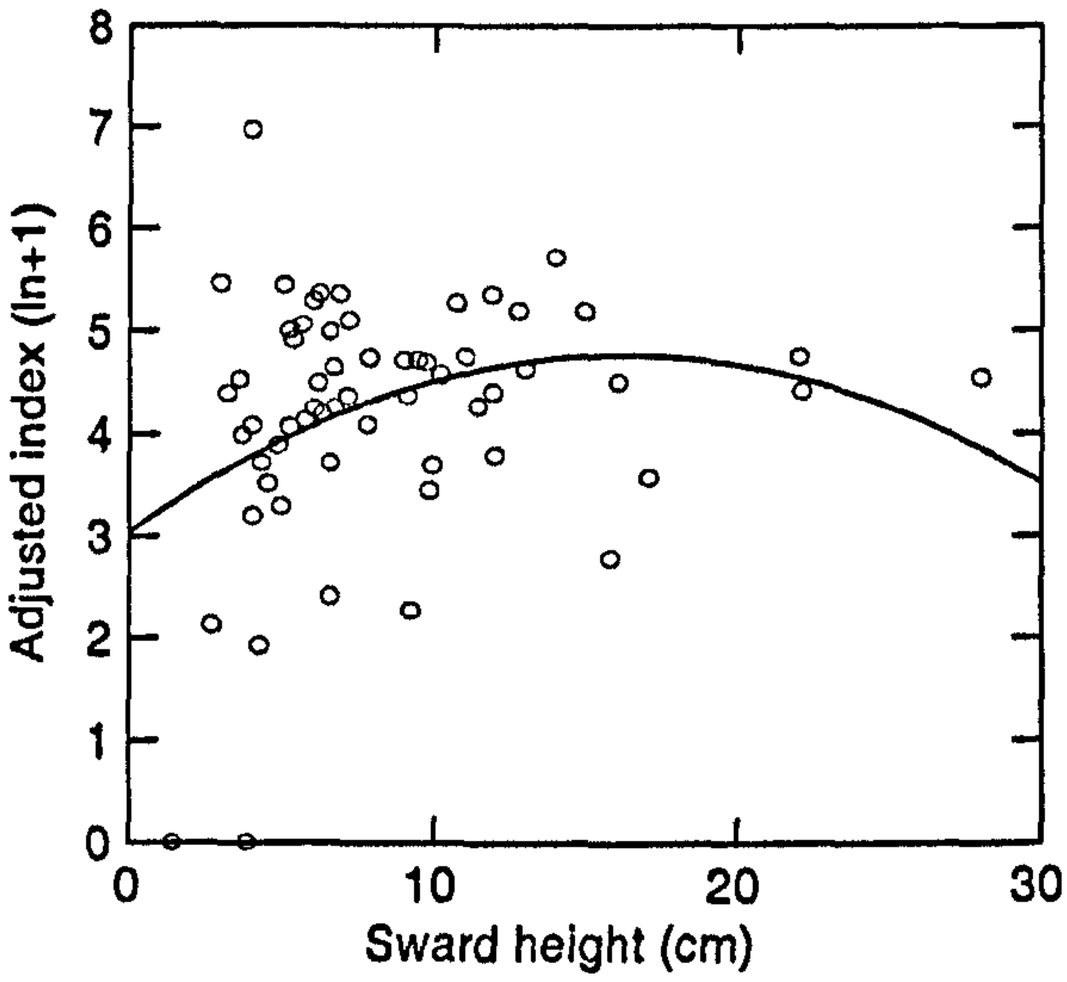
This model excluded one outlier case with an unusually high count.

This model's predictive power was tested by generating predicted populations for the 1997 Porton Down data and regressing them against observed (adjusted) populations. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.202$; $n = 67$, $P \cong 0.1$).

This is another species which has a large proportion of its flight period during late summer and this may well have affected its habitat selection behaviour during the hot and dry months of July and August1995. The model shown above includes significant parameters which are counter-intuitive to perceived meadow brown behaviour such as the avoidance of longer grassy swards in MG1 communities. This and the selection for steeper slopes, which at Porton Down tend to be those which are north-facing, points to behaviour related to avoidance of drought conditions during the summer of 1995. Inspection of relationships

at a univariate level reveals that both sward height and slope showed differences between 1995 and 1997 (Figures 4.17 a & b and 4.18 a & b). This may demonstrate the species' need to seek less desiccated areas for egg-laying as its larval food-plants (grasses) dried up.

Figure 4.17a: The relationship between adjusted population index and sward height at Porton Down in 1995 (first order polynomial regression line shown †)



† A linear relationship is not assumed in any of these Figures.

Figure 4.17b: The relationship between adjusted population index and slope at Porton Down in 1995 (first order polynomial regression line shown)

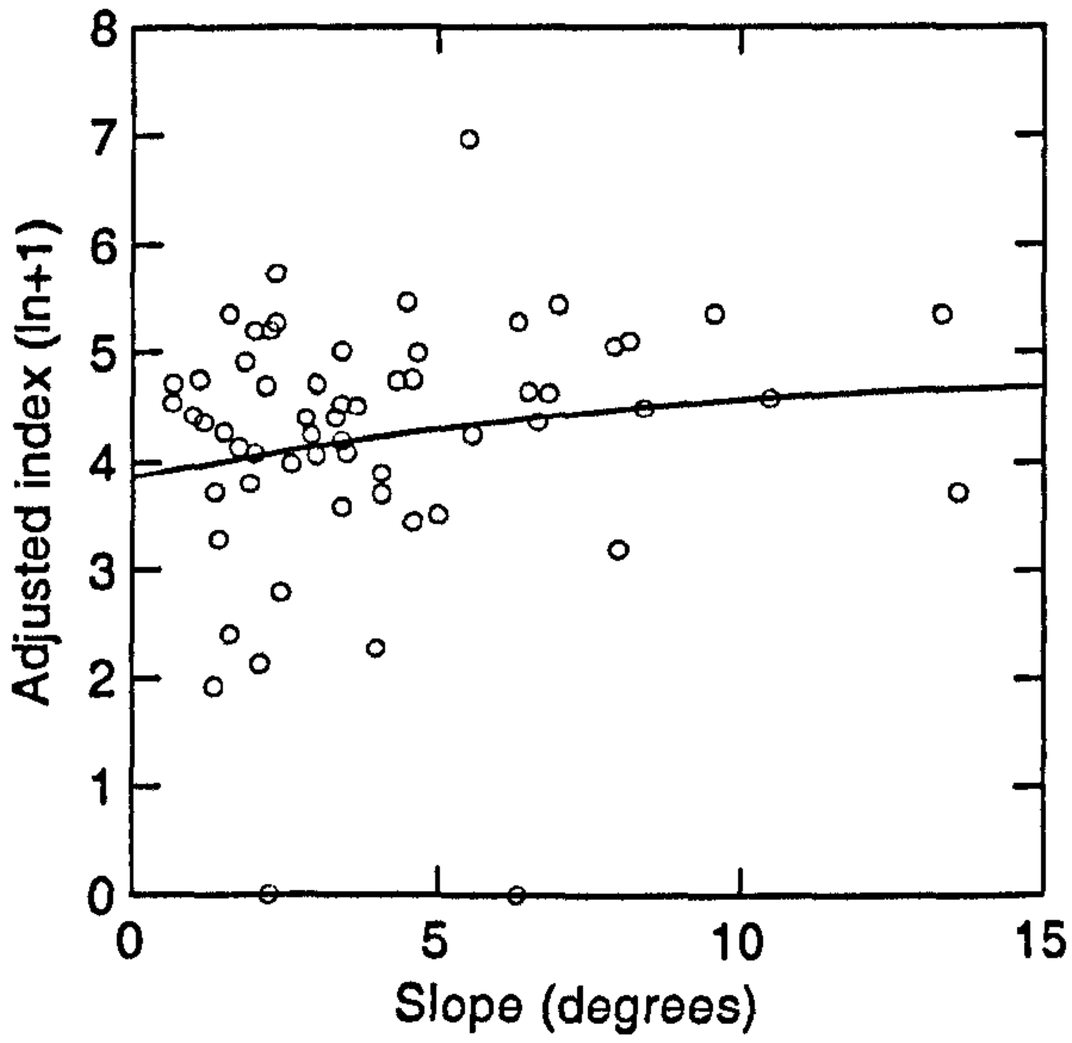


Figure 4.18a: The relationship between adjusted population index and sward height at Porton Down in 1997 (first order polynomial regression line shown)

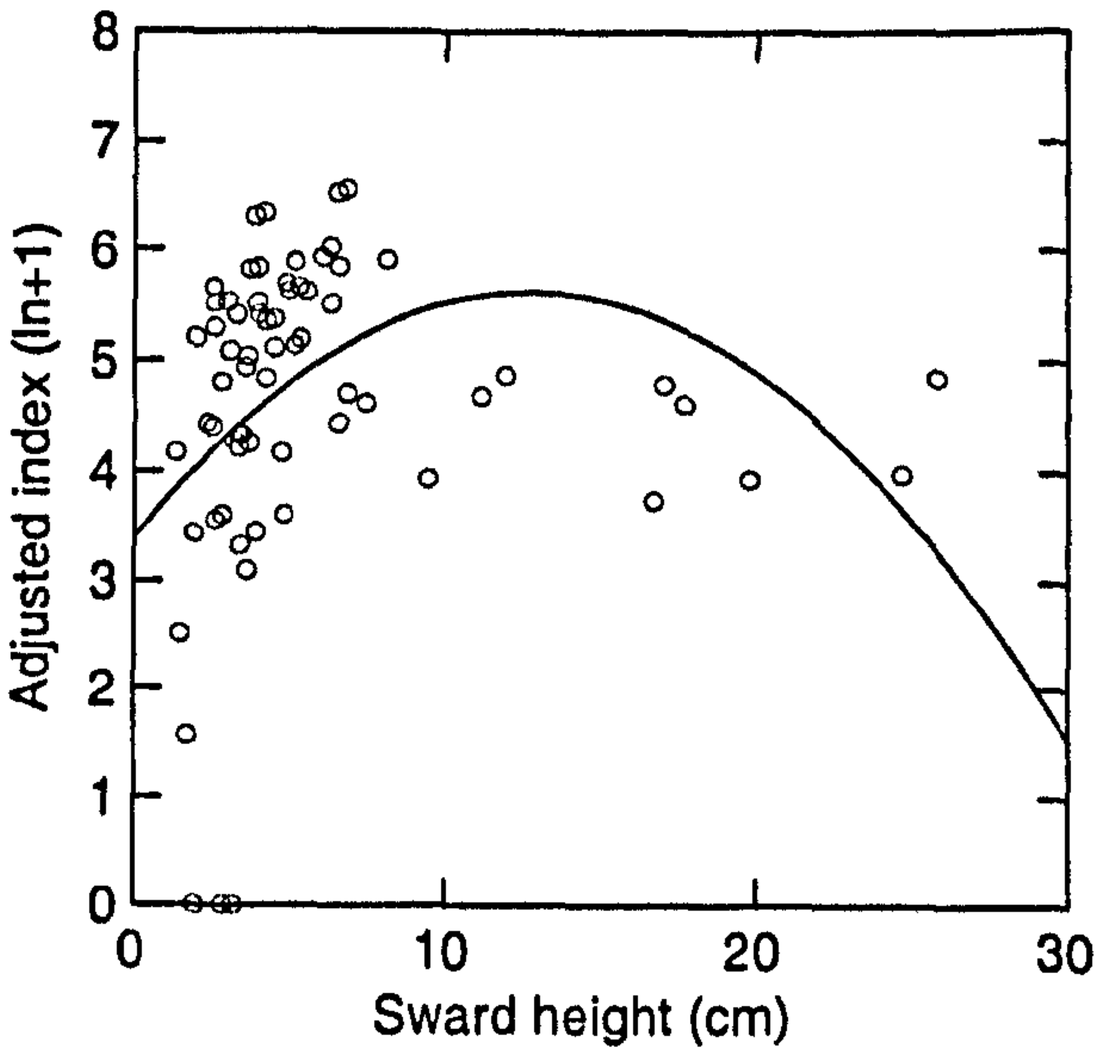
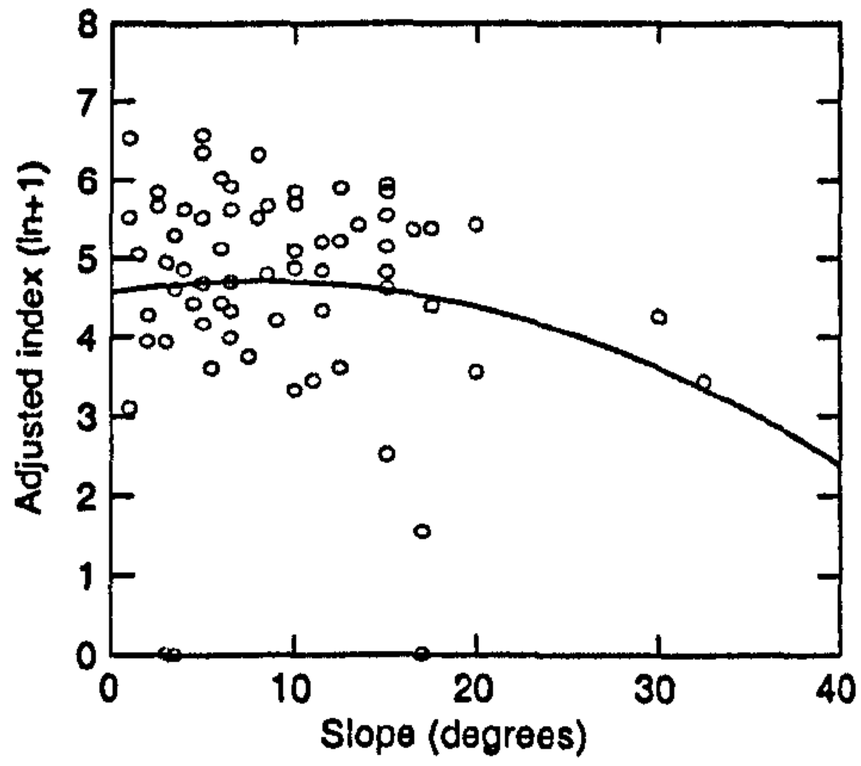


Figure 4.18b: The relationship between adjusted population index and slope at Porton Down in 1997 (first order polynomial regression line shown)



A model was subsequently produced using data for Porton Down in 1997 which was almost as warm as 1995 but much more normal in terms of rainfall (see Section 3.6). This was:

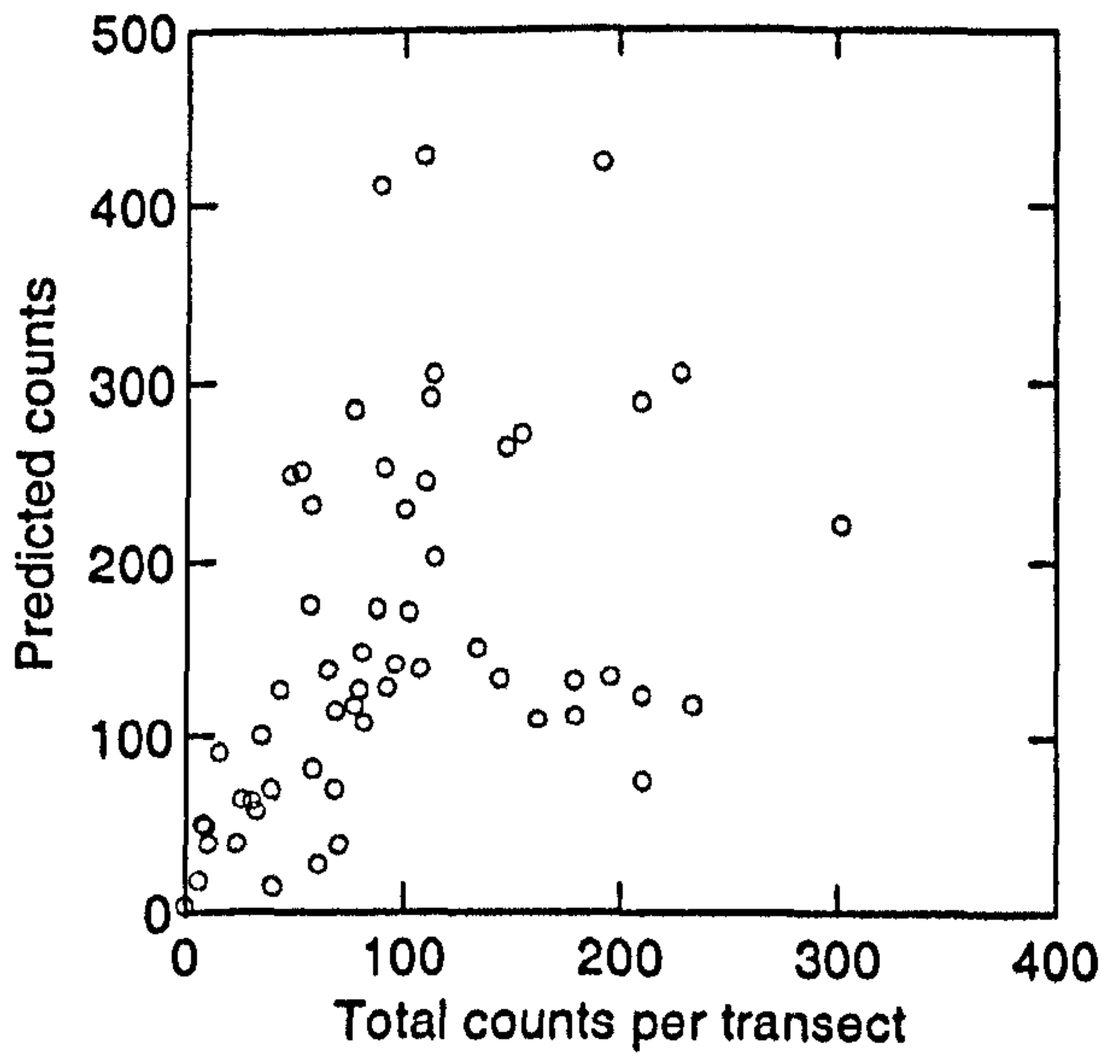
Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,61)
Constant	-5.662 (2.98)	3.611	0.06213
Aspect	0.547 (0.2622)	4.353	0.04113
Scrub	0.7917 (0.2127)	13.851	<0.001
Stones	1.456 (0.4454)	10.684	0.00178
No. Food-plants	1.138 (0.295)	14.885	<0.001
Bare*Rabbit Ind.	-0.004045 (0.0013)	9.688	0.002822

Scale parameter = 18.28; Filliben coefficient = 0.9951

This model's predictive power was tested by generating predicted populations for the 1995 Porton Down data and plotting them against observed (adjusted) populations (Figure 4.19). This plot excludes one outlier with an unusually high count. This relationship is highly significant (Spearman Rank Correlation Coefficient, $r_s = 0.605$; $n = 59$, $P << 0.001$).

There was an additional factor which may account for some of the poor predictive power of the 1995 model and that was the relatively low population in that year. The BMS Index for 1995 was 1923 but was nearly 0.5 times greater in 1997 at 2743. The 1995 Index was also up on 1994 (914) and continued to increase in 1996 (2809) so was not solely the result of within-season climatic conditions.

Figure 4.19: The relationship between predicted populations for Porton Down 1995 data and transect count totals for meadow brown



The 1997 Porton Down model therefore appears to be adequate to describe and predict meadow brown habitat selection on a between year basis.

4.25 RINGLET *Aphantopus hyperantus*

It was not possible to produce models from either 1995 nor 1997 Porton Down data as frequencies were extremely low in both data sets (4 and 2 respectively). However, the species was fairly common at Fragmented Sites and therefore a model was produced from 1996 Fragmented Site data at a local scale. This was:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-0.81931 (0.559)		
Aspect	-0.2972 (0.1077)	8.866	0.002905
Rabbit Index	-0.08092 (0.03845)	5.498	0.01904
Scrub*Nectar Sources	0.06265 (0.01516)	22.9	<0.001

(Total Model Scaled Deviance $\chi^2_3 = 30.8$; $P << 0.001$)

There were clear differences between the recording years where, in 1995, ringlets were observed 'retreating' into their optimal habitat, entirely away from open areas as hot and dry conditions ensued (Greatorex-Davies 1996). 1996 was a very much cooler and wetter summer and the species was presumably able to recolonize many of the more marginal habitats.

The model may also reflect differences in habitats where sample transects were placed. Most of these were on open grassland at Porton Down whereas there were several more scrubby/woodland edge areas on the Fragmented Sites.

The Fragmented Site model would appear to be an adequate one for descriptive and predictive purposes on a regional scale and for most normal years in terms of climate.

4.26 SMALL HEATH *Coenonympha pamphilus*

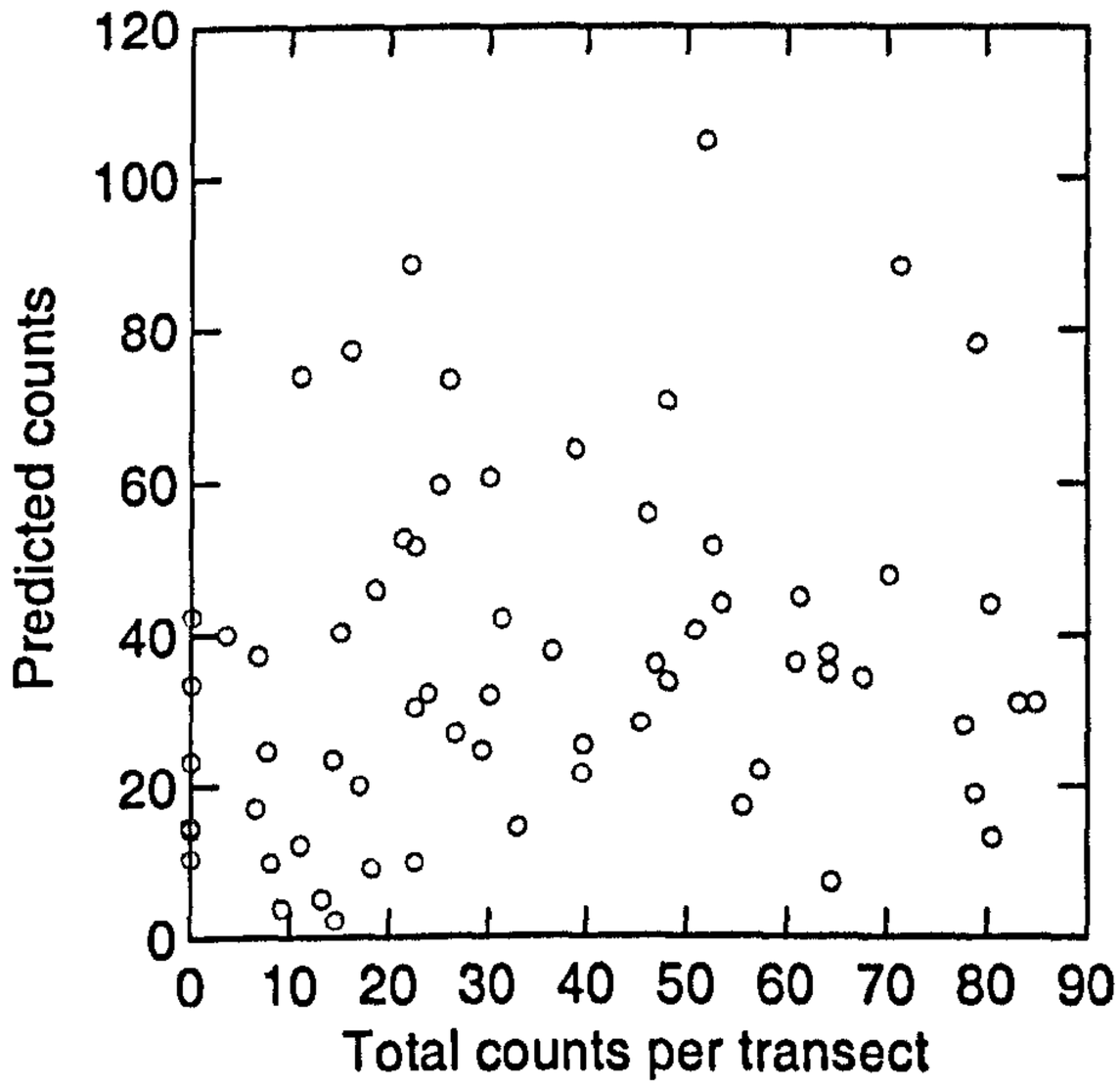
Analysis of the 1995 Porton Down data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,54)
Constant	0.2461 (0.7729)		
CG2	1.945 (0.519)	14.069	<0.001
CG3	1.935 (0.5461)	12.563	<0.001
CG6	1.706 (0.8085)	4.452	0.03951
Slope	0.222 (0.0809)	7.534	0.008204
Aspect	0.2766 (0.09587)	8.327	0.005603

Scale parameter = 2.684; Filliben coefficient = 0.9927

This model's predictive power was tested by generating predicted populations for the 1997 Porton Down data and plotting them against observed (adjusted) populations

Figure 4.20: The relationship between predicted populations for Porton Down 1997 data and transect count totals for small heath



(Figure 4.20). This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.223$; $n = 67$, $0.1 > P > 0.05$). There was a large difference between population indices recorded in the two years for small heath on the BMS (352 in 1995 and 503 in 1997, 43% higher) and this may explain the relative lack of the model's predictive power.

This model therefore appears to be adequate to describe and predict small heath habitat selection on a between year basis.

4.27 SUMMARY OF RESULTS

Table 4.1: Summary results of habitat analysis on Porton Down. (Significant variables obtained from Fragmented Site local scale analyses shown in parentheses)

Species	Significant variables included
Small skipper	((-)Rabbit Index, (-)Bare Ground)
Essex skipper	((-)Rabbit Index, Scrub, (-)Bare Ground*Stones)
Silver-spotted skipper	Presence CG6, (-)Slope, Food-plant, Nectar Sources
Large skipper	Presence CG3, (-)Aspect, Bare Ground*Sward Height, Food-plant
Dingy skipper	Aspect, Food-plant
Grizzled skipper	Presence CG7, Food-plant
Green hairstreak	Presence CG2, (-)Presence CG6, Scrub
Small copper	(-)Presence CG6, Nectar Sources
Small blue	(No Significant Variables)
Brown argus	(-)Sward Height, Scrub, Food-plant
Common blue	Sward Height*Food-plant, (-)Sward Height*Rabbit Index, (-) Sward Height*Bare Ground, Aspect
Chalkhill blue	Food-plant
Dark green fritillary	Presence CG3, Food-plant
Marbled white	Sward Height, Presence CG3, Scrub, (-)Stones
Hedge brown	Food-plant
Meadow brown	Aspect, Scrub, Stones, (-)Bare Ground*Rabbit Index, No. Food-plants

Table 4.1 (Continued)

Ringlet	((-)Aspect, (-)Rabbit Index, Scrub*Nectar Sources)
Small heath	Presence CG2, Presence CG3, Presence CG6, Slope, Aspect

4.28 DISCUSSION

Of the eighteen species with enough data to construct models, analysis of all but one (small blue) resulted in models which defined their presence or population density according to habitat and environmental variables with statistical significance. Of these seventeen, ten models showed good between-year predictive power with a further three marginal. Only three showed poor between-year predictive power (ringlet could not be tested).

The analyses demonstrate to a large degree, how 'fixed' butterflies are in terms of habitat selection and this partly reflects the ability of Lepidopterists to be able to predict species' presence in certain habitats. However, the fact that only ten of the species showed significant selection for food-plants (only two for food-plant only), demonstrates how simplistic attempts to predict and manage habitats for this feature only are. As with other invertebrate and vertebrate groups (Newton 1998), habitat selection involves a wide variety of behavioural, physiological and physical requirements to maintain the adult form (Warren 1995).

Table 4.2 shows species grouped according to their similarity of selection for habitat and environmental variables. Groups were partly assigned by a cluster analysis performed in

Systat 6.0 and partly by objective comparisons. There are three main groups, assigned according to associations with sward height, rabbit index and food-plants, with two further poorly defined groups of one and two species respectively. The three main groups do reflect a set of species associations according to broad chalk grassland types. The first group (large skipper to marbled white), could probably be combined with the second (small skipper to meadow brown), in that all species here prefer areas of long grass, although for common blue, a mixture of long and short grass areas is ideal (BUTT 1986). The third group (silver-spotted skipper to dark green fritillary), is largely characteristic of grazed chalk grasslands (BUTT 1986). Hedge brown is included in this group for the model having selected its food-plant only, but is very much more a species of sheltered areas with longer grass. Small heath could be added to this group as shown by its selection for species-rich chalk grassland NVC types, which, at Porton Down, are largely the grazed ones (see Section 3.2). The last group (green hairstreak and small copper) is due to these species' negative association with CG6 NVC type and this is probably a reflection of their preferred habitat which often includes scrubby edges (BUTT 1986).

Further analysis of species' associations with habitat and environmental variables is given in Chapter 7 ("Community Analysis").

Table 4.2: Species groupings according to similarity of selection for habitat and environmental variables

	Sward height	Rabbit index	Slope	Aspect	Scrub	Bare Ground	Stones	CG2	CG3	CG6	CG7	Food-plant	Nectar sources
Large skipper	(+)[1]			-		(+)[1]			+			+	
Common blue	(+)[1] (-)[2,3]	(-)[2]		+		(-)[3]						(+)[1]	
Marbled white	+				+		-		+				
Small skipper		-				-							
Essex skipper		-			+	(-)	(-)						
Ringlet		-		-	(+)[1]								(+)[1]
Meadow brown		(-)[1]		+	+	(-)[1]	-					+	
Small heath			+	+				+	+	+			
Silver-spotted skipper			-							+		+	+
Dingy skipper				+								+	
Grizzled skipper											+	+	
Brown argus	-				+							+	
Chalkhill blue												+	
Dark green fritillary									+			+	
Hedge brown												+	
Green hairstreak					+			+		-			
Small copper										-			+

Footnote: variables denoted as eg (+)[1] are product combinations, with overall product sign shown for both.

5. REGRESSION ANALYSIS OF BUTTERFLIES ON PORTON DOWN PATCHES

5.1 INTRODUCTION

This chapter presents analyses of butterfly presence or population density (for the commonest species) as defined by patch habitat and environmental variables. The aim of these analyses is to identify any medium-scale landscape effects. Analyses are presented by taxonomic order given in Thomas and Lewington (1991) and Chapter 4.

Details of methods used to summarise data derived from Porton Down patches are given in Section 2.5.

5.2 OVERVIEW OF ANALYSIS OF SMALL SKIPPER *Thymelicus sylvestris* and ESSEX SKIPPER *Thymelicus lineola*

The same criteria were used for including data on small and Essex skippers from fragmented sites as on Porton Down (see Section 4.2).

5.3 SMALL SKIPPER *Thymelicus sylvestris*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-4.334 (1.788)		
Food-plant	0.872 (0.4321)	5.967	0.01458

(Total Model Scaled Deviance $\chi^2_1 = 5.967$; P = 0.01458).

Predicted P-values were calculated for the 1997 Porton Down Patch data and regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.083$; n = 16, NS).

Although food-plant was not selected in the Porton Down local scale analysis, it was strongly correlated with both sward height and rabbit index and included as product variables with these in the current GLIM analysis. The process of averaging of data could have resulted in any or all of these variables being included in the model.

5.4 ESSEX SKIPPER *Thymelicus lineola*

Analysis of the 1995 Porton Down Patch data failed to produce a significant model. The nearest variables to a significant fit were the product of sward height*bare ground ($\chi^2_1 = 3.504$; P = 0.0612). (-) Bare ground was included as a significant variable in both the local scale and Fragmented Site GLIM analyses and was consistently correlated with stones, sward height and rabbit index throughout these.

5.5 SILVER-SPOTTED SKIPPER *Hesperia comma*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-6.753 (2.575)		
Slope	0.376 (0.1848)	10.57	0.001149
Nectar sources	1.001 (0.4597)	8.183	0.004228

(Total Model Scaled Deviance $\chi^2_2 = 17.45$; P = <0.001)

Predicted P-values were calculated for the 1997 Porton Down Patch data and regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = -0.021$; n = 17, NS).

Interestingly, (+)slope was selected in the Porton Down 1995 local scale GLIM analysis while nectar sources was selected from the 1997 data set when climatic conditions were more 'normal' (see Section 4.6).

5.6 LARGE SKIPPER *Ochlodes venata*

Analysis of the 1995 Porton Down Patch data failed to produce a significant model. The nearest variable to a significant fit was aspect ($\chi^2_1 = 3.182$; P = 0.07445). Aspect was one of the variables selected in the Porton Down 1995 local scale GLIM analysis.

5.7 DINGY SKIPPER *Erynnis tages*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-7.405 (2.696)		
Aspect	0.633 (0.3288)	5.224	0.02228
Food-plant	0.9243 (0.3519)	12.35	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 15.48$; P <0.001)

Predicted P-values were calculated for the 1997 Porton Down Patch data regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.016$; n = 17, NS).

The variables aspect and food-plant were the only ones selected in the Porton Down 1995 local scale GLIM analysis.

5.8 GRIZZLED SKIPPER *Pyrgus malvae*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	0.9203 (0.9676)		
Nrst Pop Node	-1.559 (0.769)	7.752	0.005365

(Total Model Scaled Deviance $\chi^2_1 = 7.752$; P = 0.005365)

It was not possible to test the model against observed 1997 data as there were too few recorded in 'test' patches, despite the species being very much more common in this year.

This landscape variable was of over-riding importance in explaining variation in the data. The next nearest variable to being included was food-plant ($\chi^2_1 = 2.939$, P = 0.08646), which was one of the local scale variables included in the Porton Down 1997.

5.9 GREEN HAIRSTREAK *Callophrys rubi*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independant variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-9.566 (32.41)		
CG2	10.56 (32.41)	11.09	<0.001

(Total Model Scaled Deviance $\chi^2_1 = 11.09$; P <0.001)

Predicted P-values were calculated for the 1997 Porton Down Patch data and regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.159$; n = 17, NS). However, high mean counts were observed in patches where there were also high predicted P-values.

Presence of CG2 was one of the significant variables selected in the Porton Down 1995 local scale GLIM analysis for this species.

5.10 SMALL COPPER *Lycaena phlaeas*

Analysis of the 1995 Porton Down Patch data failed to produce a significant model. The nearest variable to a significant fit was the product of Nrst. Pop. Node*Ave. Dist. to Nodes ($\chi^2_1 = 2.498$; P = 0.114).

5.11 SMALL BLUE *Cupido minimus*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	11.3 (5.579)		
Bare ground	-2.268 (1.204)	6.046	0.01394
Dist. To Nrst Node	-10.26 (5.19)	13.52	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 17.23$; P <0.001)

It was not possible to test the model against observed 1997 data as there were too few recorded in 'test' patches, as the species was very much less common in this year.

Bare ground was the variable which was closest ($\chi^2_1 = 2.712$; P = 0.0996) to being included in the GLIM model in the Porton Down 1995 local scale GLIM analysis for this species. However, it would seem that the inclusion of landscape scale variables greatly improves the power of the model.

5.12 BROWN ARGUS *Aricia agestis*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	0.2372 (1.206)		
Sward height	-0.6601 (0.2755)	14.35	<0.001
Scrub	1.048 (0.4648)	11.11	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 19.62$; P <0.001)

Predicted P-values were calculated for the 1997 Porton Down Patch data and regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.102$; n = 17, NS). However, the highest mean count was observed in a patch where there was also a high predicted P-value.

Sward height and scrub were two of the three significant variables selected in the Porton Down 1995 local scale GLIM analysis for this species the other being food-plant which had the next highest χ^2 value in the regression analysis ($\chi^2_1 = 2.861$; P = 0.09075). The Patch analysis therefore produced very similar results to the local scale one.

5.13 COMMON BLUE *Polyommatus icarus*

Analysis of the 1995 Porton Down Patch data failed to produce a significant model. The nearest variable to a significant fit was (-) Distance to Nearest Node ($F_{1,29} = 3.756$; P = 0.06241).

5.14 CHALKHILL BLUE *Lysandra coridon*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independant variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	2.144 (1.042)		
Ave. Dist. to Nodes	-0.7256 (0.2901)	7.636	0.005721

(Total Model Scaled Deviance $\chi^2_1 = 7.636$; P = 0.005721)

This landscape scale variable was of over-riding importance with no other variable coming near to significance for inclusion in the model.

Predicted P-values were calculated for the 1997 Porton Down Patch data and regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.206$; $n = 17$, $0.5 > P > 0.2$). However, the highest mean count was observed in a patch where there was also a high predicted P-value.

5.15 DARK GREEN FRITILLARY *Argynnis aglaja*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,28)
Constant	2.891 (0.6839)	17.87	<0.001
CG3	1.615 (0.5755)	7.875	0.009018
Food-plant	0.3946 (0.1781)	4.908	0.03504

Scale parameter = 2.282; Filliben coefficient = 0.9942

This model's predictive power was tested by generating predicted mean counts for the 1997 Porton Down patch data and regressing them against observed mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.461$; $n = 17$, $0.1 > P > 0.05$).

The GLIM patch model is remarkably similar, in both having the same selected local scale variables and the parameter estimates generated as the Porton Down 1995 local scale model.

5.16 MARBLED WHITE *Melanargia galathea*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,27)
Constant	-1.458 (0.8687)	2.818	0.1048
CG3	2.208 (0.7002)	9.946	0.003929
Sward height	0.2102 (0.07078)	8.819	0.006188
Scrub	0.3805 (0.1486)	6.56	0.01633

Scale parameter = 2.939; Filliben coefficient = 0.985

This model's predictive power was tested by generating predicted mean counts for the 1997 Porton Down patch data and regressing them against observed mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.205$; $n = 17$, $0.5 > P > 0.2$).

The local scale variables selected in the above model were also selected in the Porton Down 1995 local scale GLIM analysis, with the addition of (-) stones.

5.17 HEDGE BROWN *Pyronia tithonus*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	5.363 (2.572)		
Rabbit Index	-0.04344 (0.02185)	7.289	0.006938
Dist. To Nrst Node	-5.453 (2.251)	13.76	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 17.56$; $P < 0.001$)

Predicted P-values were calculated for the 1997 Porton Down Patch data and regressed against Porton Down Patch mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.332$; $n = 17$, $P < 0.2$). However, the highest mean count was observed in a patch where there was also a high predicted P-value.

5.18 MEADOW BROWN *Maniola jurtina*

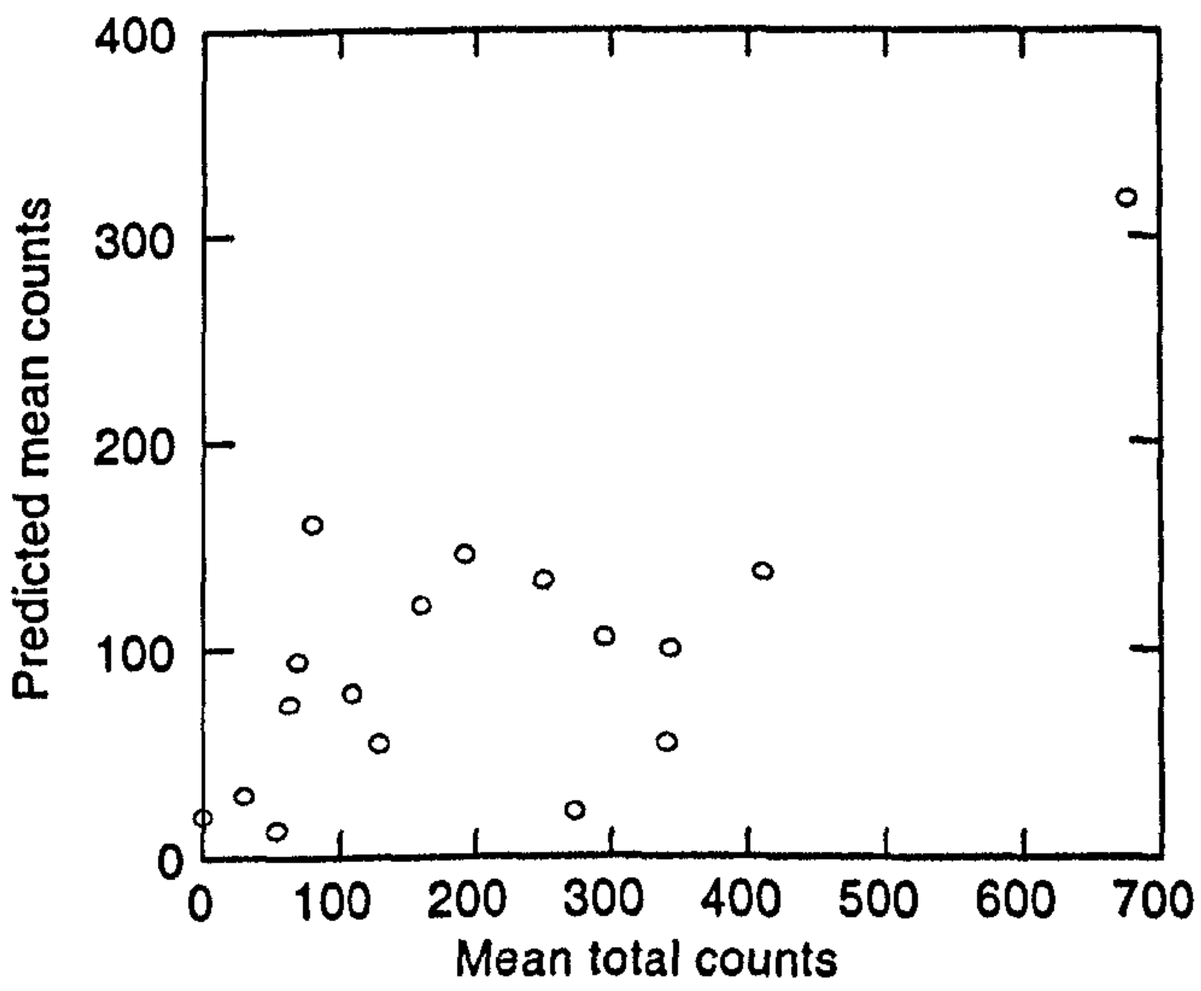
Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,28)
Constant	9.38 (1.187)	62.424	<0.001
Scrub*Nectar sources	0.1555 (0.03779)	16.93	<0.001
Dist. To Nrst Node	-2.399 (0.7811)	9.429	0.004713

Scale parameter = 9.043; Filliben coefficient = 0.9879

This model's predictive power was tested by generating predicted mean counts for the 1997 Porton Down patch data and plotting them against observed mean counts (Figure 5.1). This relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.544$; $n = 17$, $0.05 > P > 0.02$). Figure 5.1 shows that the 1995 model predicts less mean counts than were observed. This discrepancy is probably due to the general increase in numbers of this species at Porton Down between the years (see Section 4.24).

Figure 5.1: The relationship between predicted populations for Porton Down 1997 patch data and mean transect count totals for meadow brown



The 1995 Porton Down local scale model selected six variables, including nectar sources, in order to describe the variation in meadow brown numbers. It would seem that the inclusion of the landscape scale variable gives a robust and much simpler model which also has a high degree of between-year predictive power.

5.19 RINGLET *Aphantopus hyperantus*

There were insufficient data for GLIM analysis for this species.

5.20 SMALL HEATH *Coenonympha pamphilus*

Analysis of the 1995 Porton Down Patch data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,28)
Constant	4.47 (0.9294)	23.135	<0.001
Aspect	0.3001 (0.1362)	4.854	0.03598
Patch area	-0.1158 (0.04051)	8.179	0.00792

Scale parameter = 2.268; Filliben coefficient = 0.9836

This model's predictive power was tested by generating predicted mean counts for the 1997 Porton Down patch data and regressing them against observed mean counts. This relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.284$; n = 17, 0.5 > P > 0.2).

Aspect was one of the variables included in the 1995 Porton Down local scale GLIM model.

5.21 SUMMARY OF RESULTS

Table 5.1: Summary results of habitat & landscape analysis on porton down patches

	Significant variables included at two scales	
Species	Local scale	Landscape scale
Small skipper	Food-plant	
Essex skipper	(No Significant Variables)	
Silver-spotted skipper	Slope, Nectar Sources	
Large skipper	(No Significant Variables)	
Dingy skipper	Aspect, Food-plant	
Grizzled skipper		(-)Nearest Pop. Node
Green hairstreak	Presence CG2	
Small copper	(No Significant Variables)	
Small blue	(-)Bare Ground	(-)Nearest Pop. Node
Brown argus	(-)Sward Height, Scrub	
Common blue	(No Significant Variables)	
Chalkhill blue		(-)Ave. Distance to Pop. Nodes
Dark green fritillary	Presence CG3, Food-plant	
Marbled white	Sward Height, Presence CG3, Scrub	
Hedge brown	(-)Rabbit Ind.	(-)Nearest Pop. Node
Meadow brown	Scrub*Nectar Sources,	(-)Nearest Pop. Node
Ringlet	(Insufficient Data)	
Small heath	Aspect	(-)Patch Area

5.22 DISCUSSION

Of the seventeen species with enough data to construct models, analysis of thirteen resulted in models which defined their presence or population density according to patch habitat and environmental variables with statistical significance. Of these thirteen, only one model showed good between-year predictive power with one approaching marginal.

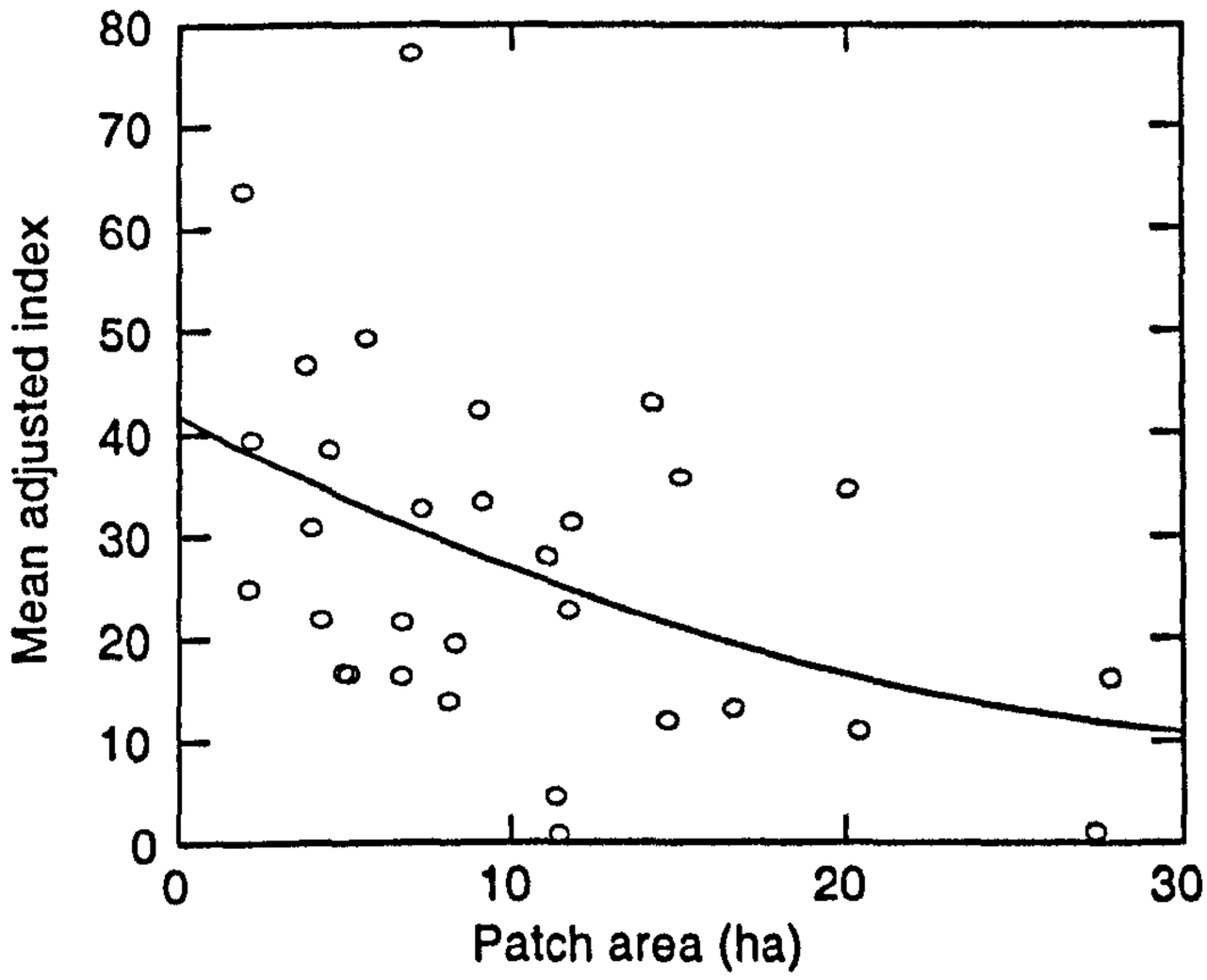
For the majority of species with significant models, local scale habitat/environmental variables were still important, with most having variables in common with the full local scale analysis (Chapter 4). The inclusion of a landscape scale variable (in six species) appeared to be associated with colonial/territorial species with relatively small, closed populations (Warren 1992; Brereton *et al* 1998) and this suggests that even within a large, contiguous block of similar habitat, patch dynamics may play a major part in population regulation. In this case, the most simple explanation for the relationships involving distance to nodes/node centres is as a surrogate for distance from the high population density core of a colony. The non-inclusion of some species which might be included in this group, such as silver-spotted skipper and dingy skipper, is logical if their colonies are more diffuse at Porton Down, reacting to widespread and relatively abundant resources. However, species such as green hairstreak would be expected to show selection for landscape scale variables, if indeed the mechanism being detected is associated with distance from the high population density core of a colony.

Table 5.2 shows species grouped according to their similarity of selection for patch habitat and environmental variables. Groups were partly assigned by a cluster analysis performed

in Systat 6.0 and partly by objective comparisons as in Table 4.2. However, there are really only two main groups, assigned according to whether selection included landscape scale variables or not. There do not appear to be any further consistent groupings.

Two species showed selection for landscape scale variables other than distance to the nearest node. Small heath showed selection for patch area. The negative relationship with patch area shown in Figure 5.2 is at first puzzling but nevertheless clear. As total patch area decreases, the total boundary length decreases even though the relative (to area) patch boundary length increases and this could be the explanation for the nature of this relationship. A preference for 'edges', of scrub or tracks and paths, has been quoted in BUTT (1986) for example. This may be a reflection of the species' requirement for mosaics of short and long turf (opp. cit.), and is possibly why three NVC grassland types were included in the Porton Down 1995 local scale model (Section 4.26). Negative density-area relationships are not uncommon in insects (Connor *et al* 2000), and other effects such as social interaction and predation rates as well as spatial scaling of habitat selection (as above) have all been proposed as underlying causes (Bowers and Matter 1997).

Figure 5.2: The relationship between mean adjusted index and patch area for small heath on Porton Down patches in 1995 (first order polynomial regression line shown †)



† A linear relationship is not assumed

Chalkhill blue showed selection for average distance to nodes. This species is known to be able to exist in extremely small colonies (Warren 1992). This appears to be the current scenario at Porton Down where previously ideal habitat conditions due to lack of rabbit grazing had produced large colonies of many hundreds of individuals (R. Ryan pers. comm.). The greatly increased grazing pressure has reduced these colonies to several scattered ones containing only a few tens of individuals. Under this scenario, a density-distance effect would be extremely difficult to detect, but the alternative measure, average distance to nodes ('historical' population cores?), appears to be sensitive enough to detect a residual effect.

Table 5.2: Species groupings according to similarity of selection for habitat and environmental variables

	Sward height	Rabbit index	Slope	Aspect	Scrub	Bare ground	CG2	CG3	Food plant	Nectar sources	Nrst. pop. node	Ave. dist.-nodes	Patch area
Brown argus	-				+								
Silver-spotted skipper			+							+			
Dingy skipper				+					+				
Small skipper									+				
Green hairstreak							+						
Dark green fritillary								+	+				
Marbled white	+				+			+					
Meadow brown					$(+)^1$					$(+)^1$	-		
Hedge brown		-									-		
Small blue						-					-		
Grizzled skipper											-		
Chalkhill blue												-	
Small heath				+									-

Footnote: variables denoted as eg $(+)^1$ are product combinations, with overall product sign shown for both.

6. REGRESSION ANALYSIS OF BUTTERFLIES ON FRAGMENTED SITES

6.1 INTRODUCTION

This chapter presents analyses of butterfly presence or population density (for the commonest species), as defined by habitat, environmental and landscape variables and therefore defines species' presence or abundance at the landscape scale. The aim of these analyses is to identify landscape-scale effects of patch (site) area and inter-patch distance while also accounting for local scale habitat selection. Analyses are presented by taxonomic order given in Thomas and Lewington (1991) and Chapters 4 and 5.

Details of methods used to summarise data derived from Fragmented Site patches are given in Section 2.5.

6.2 OVERVIEW OF ANALYSIS OF SMALL SKIPPER *Thymelicus sylvestris* and ESSEX SKIPPER *Thymelicus lineola*

The same criteria were used for including data on small and Essex skippers from fragmented sites as on Porton Down (see Section 4.2).

6.3 SMALL SKIPPER *Thymelicus sylvestris*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	2.644 (1.496)		
Rabbit Index	-0.9605 (0.5123)	9.307	0.002283
Bare Ground	-0.8926 (0.3902)	6.384	0.01152
Sward Ht*Rabbit Ind.	0.1057 (0.0711)	4.047	0.04425
Patch Area	0.1803 (0.1123)	8.303	0.003958

(Total Model Scaled Deviance $\chi^2_4 = 21.9$; $P < 0.001$)

Predicted P-values were calculated for the 1997 Fragmented Site data and regressed against Fragmented Site transect count means. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.073$; $n = 12$, NS). As shown by the 1997 Porton Down data small skippers were very scarce in this year (frequency of 3 out of 12 Fragmented Sites a were useable for this species). This may have affected the testing of the 1996 model.

6.4 ESSEX SKIPPER *Thymelicus lineola*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-0.03171 (1.265)		
Scrub	0.4044 (0.2192)	4.483	0.03423
Bare Ground	-0.5918 (0.2457)	7.528	0.006075

(Total Model Scaled Deviance $\chi^2_2 = 10.07$; P = 0.006506)

To test the predictive power of the model, predicted P-values were calculated for the 1997 Fragmented Site data and regressed against transect count means. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.222$; n = 12, NS).

6.5 SILVER-SPOTTED SKIPPER *Hesperia comma*

Silver-spotted skippers were seen on only one Fragmented Site in 1996 and one in 1997 during this study. A colony was present at another site, Broughton Down, during the entire study period, but no butterflies were seen there during survey work. It is known that the species is also present in very low numbers at four other sites. This species has a high profile due to its national rarity (Barnett and Warren 1995) and surveyors tend to make special efforts to find individuals on sites where long-term survival probability is low.

In order to investigate how the known distribution of silver-spotted skippers fits the available habitat on Fragmented Sites, the Porton Down local scale model was used to generate predicted probabilities for all 42 Fragmented Sites surveyed in 1996. This

showed that only one of the five highest predicted probabilities (P > 0.8) included a site with a colony, although this colony, at Broughton Down, is the strongest outside Porton Down. Broughton Down is also the only one of these high probability sites with a good landscape link with Porton Down (3.18 km boundary-boundary with a number of intervening fragmented sites as potential 'stepping stones'). Although this result is probably clouded by within-site availability of suitable habitat, it does strongly suggest that landscape scale factors are an important feature of silver-spotted skipper distribution. This has already been clearly shown in a number of pieces of work on this species (see Thomas and Jones 1993; Hill *et al* 1996).

6.6 LARGE SKIPPER *Ochlodes venata*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	1.182 (0.7758)		
Aspect	-0.3934 (0.1879)	5.437	0.01971
Patch Area*Area CG3	0.6285 (0.4289)	14.34	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 17.81$; $P < 0.001$)

Predicted P-values for 1997 Fragmented Sites were generated from the 1996 Fragmented Site model and regressed against mean counts on the same transects. This showed a non-

significant relationship, (Spearman Rank Correlation Coefficient, $r_s = 0.339$; $n = 12$, $0.5 > P > 0.2$). However, the 1996 model does predict high probabilities where the large skipper occurred on Fragmented Sites in 1997, which, as with small skipper, was a poor year for this species locally (Porton Down BMS Index of 4 in 1997 compared to 15 in 1996).

6.7 DINGY SKIPPER *Erynnis tages*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-3.57 (1.331)		
Stock Grazing	-2.492 (1.404)	4.346	0.0371
Food-plant	0.7423 (0.366)	6.274	0.01225
Patch Area	0.1952 (0.09686)	8.801	0.003011

(Total Model Scaled Deviance $\chi^2_3 = 18.32$; $P < 0.001$)

When the model was tested by generating predicted P-values from the 1997 Fragmented Site data set and regressing these against mean counts on the same transects, there was no relationship, (Spearman Rank Correlation Coefficient, $r_s = 0.022$; $n = 12$, NS). This species was found on only two Fragmented Sites in 1997, one of which had a high predicted probability of occurrence. This species did not show a decline locally between

these years. It would seem that other factors might be involved in the absence of dingy skippers from the Fragmented Sites surveyed in 1997

6.8 GRIZZLED SKIPPER *Pyrgus malvae*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-2.303 (0.6014)		
Area CG2	0.554 (0.2294)	14.51	<0.001

(Total Model Scaled Deviance $\chi^2_1 = 14.51$; $P < 0.001$).

When the model was tested by generating predicted P-values from the 1997 Fragmented Site data set and regressing these against mean counts on the same transects, there was no relationship, (Spearman Rank Correlation Coefficient, $r_s = 0.394$; $n = 12$, $0.5 > P > 0.2$). This species was recorded on only one Fragmented Site during 1997, despite both a local increase (Porton Down BMS Index of 25 in 1996, 86 in 1997) and national increase (Greatorex-Davies and Pollard 1997). Predicted probabilities for the 1997 Fragmented Sites were generally low however and rapid colonization from other, more suitable sites might not be expected.

6.9 GREEN HAIRSTREAK *Callophrys rubi*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-3.649 (1.277)		
Food-plant	0.4928 (0.2297)	6.102	0.0135
Patch Area	0.1634 (0.08517)	8.815	0.002988

(Total Model Scaled Deviance $\chi^2_2 = 14.92$; $P < 0.001$)

Predicted P-values were calculated for the 1997 Fragmented Site data and regressed against site mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = -0.131$; $n = 12$, NS).

As with grizzled skipper, this species was recorded on only one Fragmented Site in 1997 and had been showing a steady decline locally since 1995 (Porton Down BMS 44 in 1995, 18 in 1996, 8 in 1997). This trend was not reflected nationally however (Greatorex-Davies and Pollard 1997).

6.10 SMALL COPPER *Lycaena phlaeas*

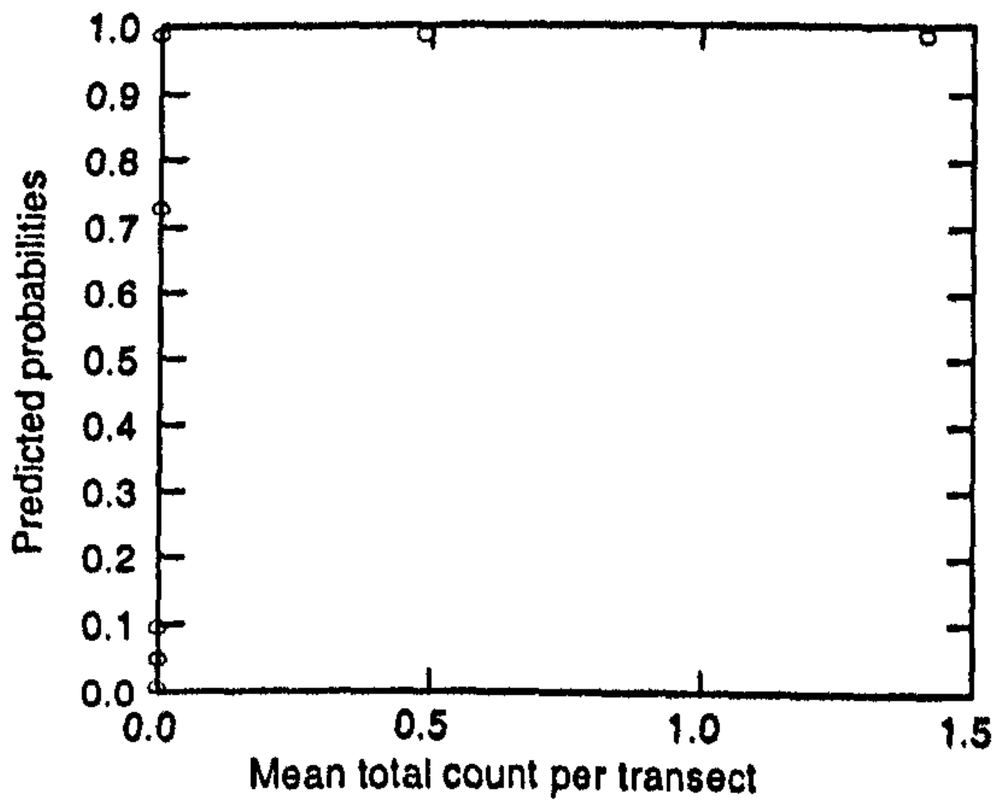
Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-2.259 (0.7536)		
Area CG6	2.193 (2.053)	5.746	0.01653
Stock Grazing	-2.917 (1.784)	4.07	0.04365
Food-plant	1.62 (0.6958)	8.1	0.004427

(Total Model Scaled Deviance $\chi^2_3 = 14.54$; $P = 0.002255$)

Predicted P-values were calculated for the 1997 Fragmented Site data and are shown plotted against site mean counts in Figure 6.1. This relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.6$; $n = 12$, $P < 0.05$). This test is again based on very few (three) sites where the species was observed in 1997 but it does correctly predict sites where probability of presence is high (Figure 6.1).

Figure 6.1: The relationship between predicted P-values generated from 1997 Fragmented Site patch data and transect count mean totals for small copper



6.11 SMALL BLUE *Cupido minimus*

This species was found on only three Fragmented Sites in 1996 and one in 1997. Although the small blue was acknowledged to be generally common in 1994 throughout its Wiltshire haunts (Fuller 1995), a subsequent decline appeared to set in which is reflected in the Porton Down BMS data (see Section 4.12).

The boom and bust nature of its one food-plant, kidney vetch *Anthyllis vulneraria*, appears to give rise to asynchronous population fluctuations (Morton 1985) among its colonies. There are no known large colonies among the Fragmented Sites in this study area (Fuller 1995) so the lack of records was probably not a function of temporarily low populations in any case.

6.12 BROWN ARGUS *Aricia agestis*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-1.539 (0.4728)		
Bare Ground*Food-plant	0.1298 (0.04716)	11.93	< 0.001

(Total Model Scaled Deviance $\chi^2_1 = 11.93$; $P < 0.001$)

Predicted P-values were calculated for the 1997 Fragmented Site data and regressed against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.408$; $n = 12$, $P \cong 0.2$). This species was only recorded at two Fragmented Sites in 1997 and show high predicted probabilities (> 0.7) at these sites. The test of the 1996 model should therefore be seen as moderately successful.

6.13 COMMON BLUE *Polyommatus icarus*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,55)
Constant	1.379 (1.377)	1.003	0.3226
Food-plant	1.005 (0.3118)	10.398	0.002514

Scale parameter = 16.6; Filliben coefficient = 0.9663

When predicted populations for 1997 Fragmented Site data are generated from the 1996 Fragmented Site model and regressed against observed site transect mean counts, this relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = -0.121$; $n = 12$, NS).

This is a widespread species of both open grassland and woodland rides in the region and although the model above reflects both the findings on Porton Down (Section 4.14) and

general knowledge of its requirements (management for its leguminous larval food-plants BUTT 1986), the explanation for the lack of relationship between years and sites must lie elsewhere.

6.14 CHALKHILL BLUE *Lysandra coridon*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-1.41 (0.4501)		
Food-plant	0.8676 (0.3117)	11.75	<0.001

(Total Model Scaled Deviance $\chi^2_1 = 11.75$; $P < 0.001$)

Predicted P-values were generated from this model for the Fragmented Site 1997 data and regressed against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.435$; $n = 12$, $0.2 > P > 0.1$). However, two of the three sites where the species was present had high (>0.9) predicted probabilities.

As with the local scale models, the important feature of this landscape scale model is that the food-plant has again been selected as the single important variable.

6.15 ADONIS BLUE *Lysandra bellargus* and 6.16 DUKE OF BURGUNDY *Hamaeris lucina*

There were insufficient data from any year to perform modelling for these species.

6.17 DARK GREEN FRITILLARY *Argynnis aglaja*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	1.2 (0.4889)		
Distance from Porton* Average Dist. From All Sites	-0.03113(0.01247)	7.674	0.005602

(Total Model Scaled Deviance $\chi^2_1 = 7.674$; P = 0.005602)

This model's predictive power was tested by generating predicted probabilities for the 1997 Fragmented Site data and regressing them against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.458$; n = 12, $0.2 > P > 0.1$), although all sites where the species was present had some of the highest predicted probabilities.

Despite the lack of between-year predictive power shown above, the significance level of the model would seem to provide strong evidence for an over-riding landscape effect for this species.

6.18 MARSH FRITILLARY *Euphydryas aurinia* and 6.19 WALL *Lasiommata megera*

There were insufficient data from any year to perform modelling for this species.

6.20 MARBLED WHITE *Melanargia galathea*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,38)
Constant	3.999 (1.371)	8.514	0.00589
Rabbit Index	-0.1911 (0.09076)	4.432	0.04194
Scrub	0.6581 (0.2055)	10.256	0.002755
Bare Ground*Stones	-0.1069 (0.04773)	5.016	0.03104

Scale parameter = 9.858; Filliben coefficient = 0.9927

This model's predictive power was tested by generating predicted populations for the 1997 Fragmented Site data and regressing them against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.285$; $n = 12$, $0.5 > P > 0.2$).

This model is not dissimilar to the Porton Down local scale one where scrub and stones were selected with sward height which is very strongly correlated with rabbit index and bare ground (selected here). Clearly, local scale variables are an over-riding feature even at the landscape level.

6.21 GRAYLING *Hipparchia semele*

There were insufficient data from any year to perform modelling for this species.

6.22 HEDGE BROWN *Pyronia tithonus*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,39)
Constant	0.9352 (1.002)	0.87	0.3567
Scrub	0.6797 (0.1609)	17.838	<0.001
Sward Height*Rabbit	-0.0264 (0.01085)	5.919	0.01967

Scale parameter = 6.004; Filliben coefficient = 0.9843

This model's predictive power was tested by generating predicted populations for the 1997 Fragmented Site data and regressing them against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.453$; n = 12,

0.2 > P > 0.1). However, four of the five highest predicted populations had the highest observed populations so the model did show moderately high predictive power.

The variables selected in this model largely reflect the habitat available to this species at the Fragmented Sites where there was much more scrub and rank ungrazed scrub edge, even in the middle of the grassland patches.

6.23 MEADOW BROWN *Maniola jurtina*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Estimate (s.e.)	Deletion test F-statistic	Probability (all df =1,39)
Constant	5.265 (2.482)	4.499	0.04033
Stock-grazing	-4.477 (1.995)	5.036	0.03057
No. Food-plants	0.8905 (0.275)	10.489	0.002456

Scale parameter = 32.92; Filliben coefficient = 0.9804

This model's predictive power was tested by generating predicted populations for the 1997 Fragmented Site data and regressing them against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = -0.27$; n = 12, 0.5 > P > 0.2) and in fact, the model seems to over-predict populations despite the general increase in numbers indicated by counts at Porton Down (see Section 4.24) and elsewhere locally (Fuller 1999).

Number of food-plants, i.e. diversity of grasses, is the most strongly selected variable in this analysis, as was the case in the Porton Down local scale analysis (Section 4.24). The only other consistently selected element is that of grazing, which was dominated by rabbits at Porton Down and by domestic stock on the Fragmented Sites.

6.24 RINGLET *Aphantopus hyperantus*

Analysis of the 1996 Fragmented Site data produced the following model:

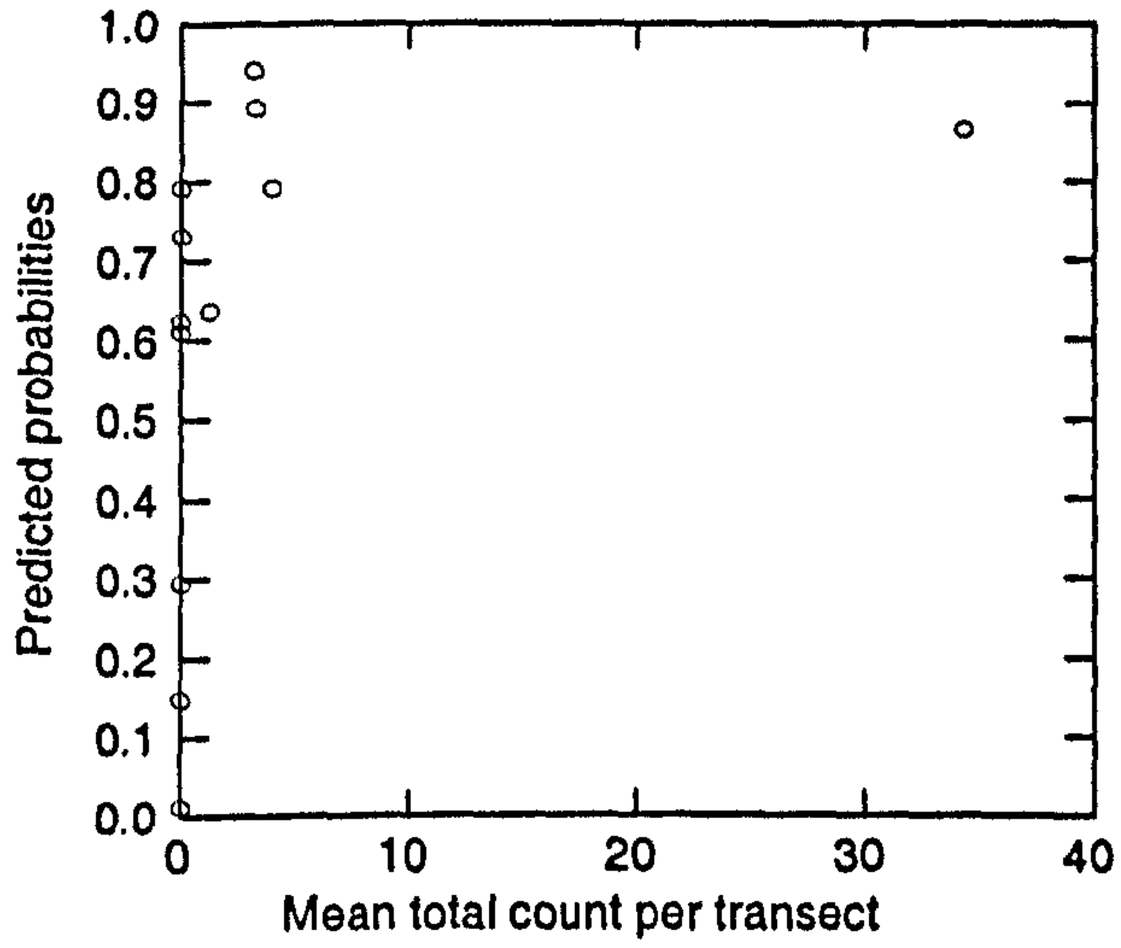
Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-4.629 (2.507)		
Aspect	-0.3311 (0.1694)	4.24	0.03948
Nectar Source	1.103 (0.4362)	11.73	<0.001

(Total Model Scaled Deviance $\chi^2_2 = 15.97$; $P < 0.001$)

Predicted P-values were generated from this model for the Fragmented Site 1997 data and plotted against observed site transect mean counts (Figure 6.2). This relationship is significant (Spearman Rank Correlation Coefficient, $r_s = 0.738$; $n = 12$, $P < 0.01$. The 1996 model appears therefore to have very high predictive power between years and sites.

Both (-) aspect and nectar sources were strongly selected for in the local scale analysis which was derived from Fragmented Site data.

Figure 6.2: The relationship between predicted P-values generated from 1997 Fragmented Site patch data and transect count mean totals for ringlet



6.25 SMALL HEATH *Coenonympha pamphilus*

Analysis of the 1996 Fragmented Site data produced the following model:

Independent variable	Logit estimate (s.e.)	Change in scaled deviance χ^2	Probability (all df =1)
Constant	-1.333 (0.4993)		
Area CG2*Area CG6	6.702 (5.56)	4.445	0.035
Patch Area	0.2236 (0.1268)	7.444	0.006365

(Total Model Scaled Deviance $\chi^2_2 = 15.2$; $P < 0.001$)

Predicted P-values were generated from this model for the Fragmented Site 1997 data and regressed against site transect mean counts. This relationship is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.177$; n = 12, NS. For this species, the 1996 model appears therefore not to have very high predictive power between years and sites.

This was one of only five species to show a significant relationship with patch area in these analyses. The inclusion of CG2 is not surprising given the strength of the relationship at the local scale, with CG6 included as a strongly correlated variable.

6.26 SUMMARY OF RESULTS

Table 6.1: Summary results of habitat & landscape analysis on fragmented sites

	Significant variables included at two scales	
Species	Local scale	Landscape scale
Small skipper	(-)Rabbit Index, (-)Bare Ground, Sward Height* Rabbit Index	Patch Area
Essex skipper	(-)Bare Ground, Scrub	
Silver-spotted skipper	[Insufficient data]	
Large skipper	(-)Aspect	Patch Area*Area CG3
Dingy skipper	Food-plant, (-)Stock Grazing	Patch Area
Grizzled skipper	Area CG2	
Green hairstreak	Food-plant	Patch Area
Small copper	Area CG6, Food-plant, (-)Stock Grazing	

Table 6.1 (Continued)

Small blue	[Insufficient data]	
Brown argus	Bare Ground*Food-plant	
Common blue	Food-plant	
Chalkhill blue	Food-plant	
Dark green fritillary		(-)Distance from Porton Down*Ave. Distance Between Patches
Marbled white	(-)Rabbit Index, Scrub, (-)Bare Ground*Stones	
Hedge brown	Scrub, (-)Sward Height* Rabbit Index	
Meadow brown	No. Food-plants, (-)Stock Grazing	
Ringlet	(-)Aspect, Nectar Sources	
Small heath	Area CG2*Area CG6	Patch Area

6.27 DISCUSSION

Analysis of all sixteen species with enough data to construct models resulted in models which defined their presence or population density according to patch habitat and environmental variables with statistical significance. Of these, only two models showed good between-year predictive power.

Of these sixteen species, only six showed any association with landscape scale variables, the rest selecting habitat/environmental variables, albeit at the whole-patch scale. Of these six, only one, dark green fritillary, showed selection for inter-patch distance. The remaining five showed selection for patch area only of the landscape scale variables.

Species groupings according to similarity of selection for habitat, environmental and landscape variables are shown in Table 6.2. Group selection criteria were the same as in sections 4.28 and 5.22. Two main groups arise from selection for habitat variables. The first, Essex skipper, marbled white and hedge brown appear to be strongly associated with scrub and indicators of low rabbit grazing on the Fragmented Sites. For Essex skipper and marbled white, general selection of variables at the landscape patch scale was very similar to that at the local scale on Porton Down (Table 4.2), suggesting that population regulation for these species is very much at the finer, habitat and local resource scale. The second group, common blue, chalkhill blue, brown argus and small copper show strong associations with their food-plants. All except small copper also selected food-plant at the local scale on Porton Down, although other differences exist between the two analyses (see Table 4.2).

The third main group, small skipper, large skipper, dingy skipper, small heath and green hairstreak, all selected patch area. It is very noticeable, that four of these species also selected either area of NVC types as preferred habitat or food-plant. Area of NVC showed strong intra-set correlations (directly with patch area in the case of large skipper), while the food-plants of both dingy skipper and green hairstreak were relatively rare on the Fragmented Sites. For this whole group, therefore, a direct positive correlation between patch size and level of resources for breeding is intimated.

The one species which stands out from this analysis is dark green fritillary. This species was the only one which selected the isolation measures, distance from Porton Down (the major 'source' site) and average distance between patches, as a product combination. This product relationship was negative, indicating that the species is extremely sensitive to

distance from major and minor 'source' populations. In addition, no local scale habitat or environmental variables were selected, despite these featuring very strongly in the previous analyses (see Tables 4.2 and 5.2). Very little is known about this relatively widespread butterfly in terms of movements and metapopulation dynamics. It is generally known to range widely within habitat patches and is a strong flier, both of which can be corroborated by observations at Porton Down. However, only one site, site K within a few hundred metres of the boundary of Porton Down, was observed to receive individuals which were crossing a main road and travelling along a grassy bank containing good nectar sources. Further analysis will hopefully reveal this species' relative sensitivity to local and landscape scale effects.

Table 6.2: Species groupings according to similarity of selection for habitat, environmental and landscape variables

	Sward height	Rabbit index	Aspect	Scrub	Bare ground	Stones	Area CG2	Area CG3	Area CG6	Food plant	Nectar sources	Stock grazing	Dist. Porton Down	Ave. dist. betw. patches	Patch area
Essex skipper				+	-										
Marbled white		-		+	$(-)^1$	$(-)^1$									
Hedge brown	$(-)^1$	$(-)^1$		+											
Grizzled skipper							+								
Ringlet			-								+				
Common blue										+					
Chalkhill blue										+					
Brown argus					$(+)^1$					$(+)^1$					
Small copper									+	+		-			
Dark green fritillary													(-)	$(-)^1$	
Small skipper	$(+)^1$	- $(+)^1$			-										+
Large skipper			-					$(+)^1$							$(+)^1$
Small heath							$(+)^1$		$(+)^1$						+
Dingy skipper										+		-			+
Green hairstreak										+					+

Footnote: variables denoted as eg $(+)^1$ are product combinations, with overall product sign shown for both.

7. BUTTERFLY COMMUNITY ANALYSIS

7.1 INTRODUCTION

This chapter extends the species' analyses to multivariate analysis where each species' presence or relative abundance places them in ordination space relative to other species in the community (Hill and Gauch 1980) and through using the canonical correspondence analysis (CCA) method (ter Braak 1987a & b), is also explained by a combination of environmental variables. The CCA package CANOCO (ter Braak 1987a and see Section 2.5.4) is used for all analyses.

7.2 PORTON DOWN LOCAL SCALE DATA

Table 7.1 shows the results of a CCA analysis using CANOCO on the Porton Down 1995 transect data. Figures in brackets are the ranks of the four highest ranking inter-set correlations of environmental variables with the axes.

The first axis accounted for 50 percent of the species-environment relationship while the second axis accounted for a further 15.8 percent only. An unrestricted Monte Carlo test was carried out on axis 1 and was significant at $P = 0.01$. This showed that the relationship between the species and environmental variables was not random on this, the most important axis. Also, calculated inflation factors showed that correlations among environmental variables was not a problem in this analysis (all inflation factors < 3.5).

Table 7.1: Results of CANOCO analysis of the Porton Down 1995 transect data

	Axis			
	1	2	3	4
Eigenvalue	0.246	0.078	0.048	0.039
Species-env. correlations	0.870	0.794	0.734	0.670
Cumulative percentage variance				
of species data	20.3	26.7	30.6	33.9
of species-env. relation	50.0	65.8	75.6	83.6
Interset correlations of environ-				
mental variables with axes (Rank):				
Sward Height	0.647 (1)	-0.423	0.780 (1)	0.500 (=2)
Rabbit Index	-0.481	0.265	-0.270	-0.131
Slope	-0.410	-0.900 (1)	-0.240	0.188
Aspect	-0.320	-0.275	0.527 (3)	0.440 (4)
Scrub	-0.112	-0.179	0.145	-0.503 (1)
Bare	-0.211	0.442 (4)	0.560 (2)	-0.172
Stones	-0.159	0.577 (2)	0.243	-0.170
CG2	-0.367	-0.200	-0.298	-0.258
CG3	0.000	-0.542 (3)	0.470 (4)	-0.246
CG6	-0.610 (3)	-0.192	0.100	0.245
CG7	-0.19	0.279	0.149	0.500 (=2)
MG1	0.555 (4)	0.130	0.265	0.240
MG5/6	-0.630 (2)	-0.103	0.239	0.344

Figure 7.1 shows the species scores for the first two CANOCO axes with the environmental variables displayed as vectors. The vector scores were calculated from the interset correlations (Table 7.1), standard deviations of the species axes and the

eigenvalues (Ter Braak 1987). It can be seen from these biplots that the first axis is mainly correlated with sward height, the presence of MG1 communities, rabbit grazing, slope and the presence of CG3 communities. Larval grass-feeders of tall swards are located along the positive part of axis 1 and the species associated with well-grazed CG communities are located along the negative part. Axis two, which is of much less importance in explaining variation in the data (see above), is mainly correlated with bare ground, stones, aspect and sward height.

As the conditions were very different between the summer drought year of 1995 and 1997, a CANOCO analysis of the Porton Down 1997 transect data was also performed. The results are shown in Table 7.2

Comparing the ordination results reveal that both the eigenvalues and cumulative percentage variances of axis 1 of the 1997 analysis are much lower values and therefore this analysis may not have been as robust as the 1995 one. However, the species-environment correlations are high for both analyses. An unrestricted Monte Carlo test was carried out on axis 1 and was significant at $P = 0.01$ showing that the relationship between the species and environmental variables was not random on this axis. However, the associated F-ratio was smaller for this data set (5.77 for 1997 compared to 11.69 for 1995). Calculated inflation factors showed that correlations among environmental variables was not a problem in this analysis (all inflation factors < 3.2).

Figure 7.1: CANOCO plot of first two axes showing ordination of Porton Down 1995 local scale data. Environmental vectors are shown as arrows (length x2). MG5/6 not shown

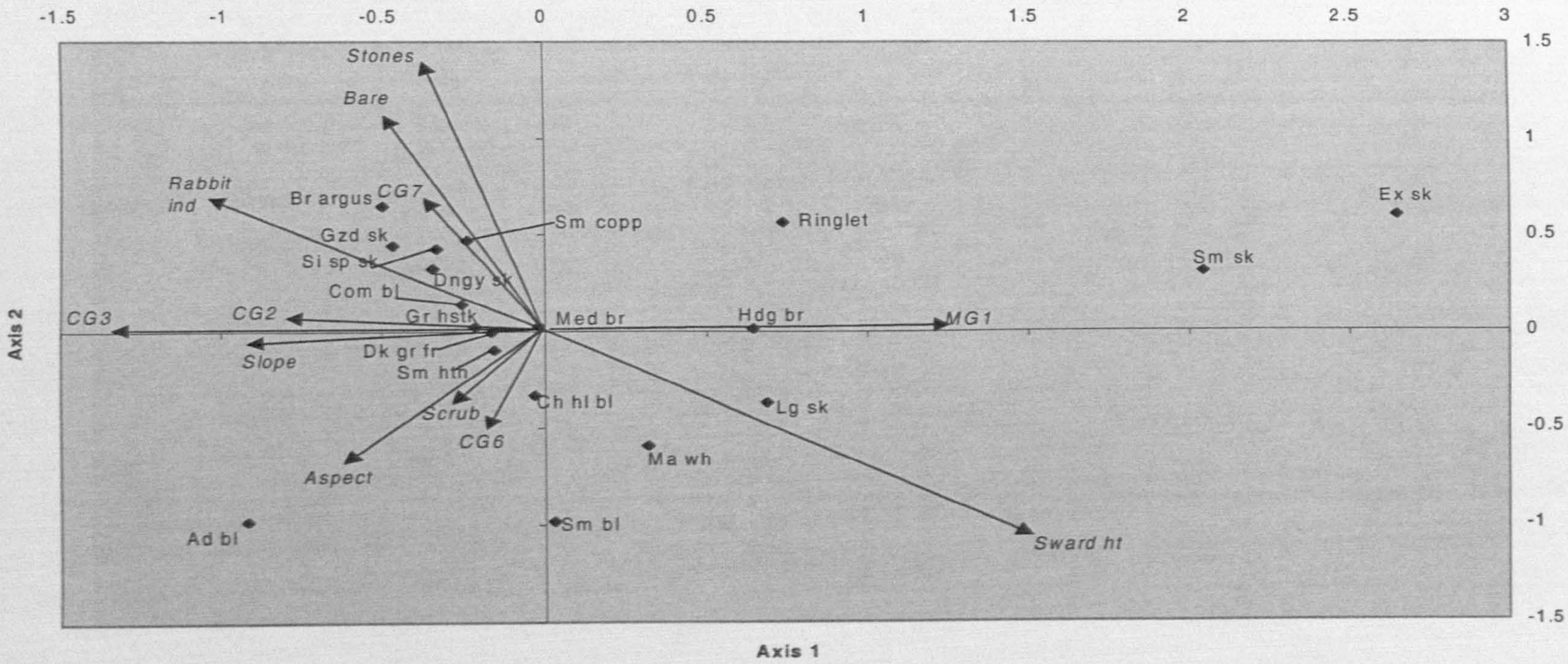


Table 7.2: Results of CANOCO analysis of the Porton Down 1997 transect data

	Axis			
	1	2	3	4
Eigenvalue	0.135	0.070	0.047	0.035
Species-env. correlations	0.812	0.743	0.645	0.674
Cumulative percentage variance				
of species data	10.0	15.2	18.6	21.2
of species-env. relation	34.2	51.9	63.8	72.6
Interset correlations of environmental variables with axes (Rank):				
Sward Height	0.642 (2)	0.267	-0.138	-0.199
Rabbit Index	0.280	-0.468	0.250	0.342
Slope	0.460	0.550	0.240	0.411
Aspect	-0.570 (3)	0.800 (2)	0.208	-0.259
Scrub	-0.116	0.880 (1)	0.425 (3)	0.875 (1)
Bare	-0.266	-0.315	0.159	0.530 (4)
Stones	-0.270	-0.159	0.142	-0.300
CG2	-0.309	-0.350	0.152	0.117
CG3	0.160	-0.210	-0.700 (1)	-0.144
CG6	0.151	-0.630 (4)	-0.230	-0.229
CG7	-0.196	0.650 (3)	-0.306 (4)	0.239
MG1	0.478 (4)	0.361	0.300	-0.700 (2)
MG5/6	0.670 (1)	-0.200	-0.470 (2)	-0.550 (3)

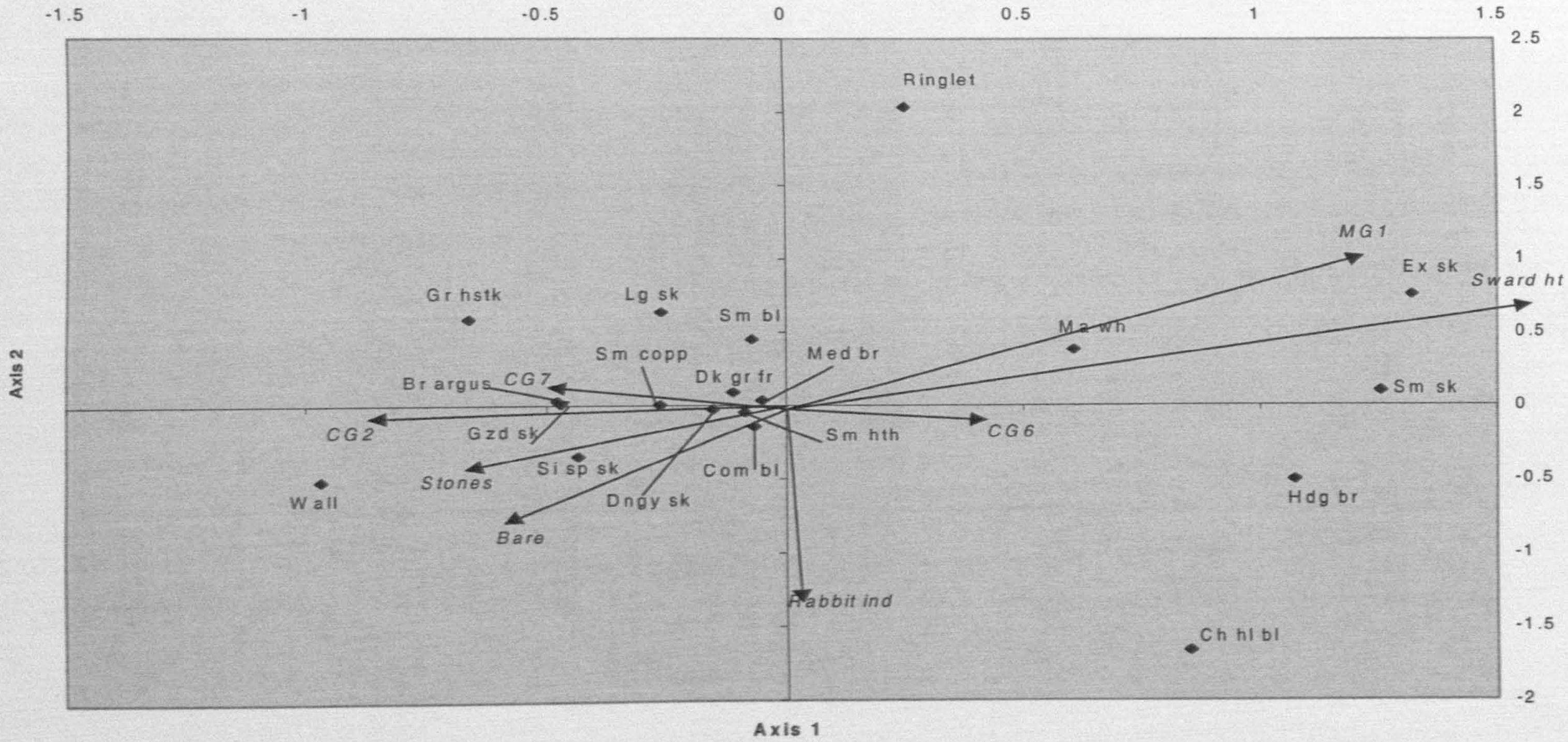
Figure 7.2 shows the species scores for the first two CANOCO axes with the environmental variables displayed as vectors for the 1997 Porton Down data. Species groupings are broadly similar to those of 1995 (Figure 7.1) with the tall sward larval grass-feeders located along the positive part of axis 1 and the species associated with well

grazed CG communities along the negative part. One species included in the 1997 analysis but not the 1995 was the wall. This species, although being a larval grass-feeder, is associated with broken turf with bare ground (BUTT 1986) and is therefore located with the bare ground and stones vectors. The position of chalk-hill blue can be explained by the fact that the species was less common in 1997 compared to 1995 (Porton Down BMS index of 15 versus 22 respectively) and had probably retreated to its preferred habitat of tall grass with some rabbit grazing which aids establishment of its food-plant *Hippocrepis comosa*. An even greater decline had occurred with large skipper (Porton Down BMS index of 4 versus 51) and small blue (Porton Down BMS index of 10 versus 45) and these species appear to have retreated totally to scrub edges on the open downland.

A very noticeable difference between the ordinations is that both the slope and aspect environmental vectors are reduced in terms of biplot scores, although aspect retains some overall influence in the ordination (Table 7.2). This reflects the major difference in climate between the years where species present during the 1995 drought period (mid to late summer) were forced to inhabit sheltered situations and avoid exposed south-facing slopes (see Chapter 4).

Figure 7.2: CANOCO plot of first two axes showing ordination of Porton Down 1997 data. Environmental vectors shown as arrows (length x2).

CG3, MG5/6, aspect, slope not shown



A further difference between the 1995 and 1997 situation was that stock grazing had been re-introduced to some areas of the downland. A separate analysis was therefore performed on the Porton Down 1997 data including stock grazing as an environmental variable and the results are shown in Table 7.3

These results are very similar to the previous ordination. The addition of stock grazing has made some difference to the power of the ordination with an increase in the eigenvalue and species-environment correlation of axis 1.

Stock grazing also ranks sixth among the interset correlations of environmental variables with axes so its inclusion appears significant. A Monte-Carlo test again proved significant (P = 0.01) for axis 1 with a slightly improved F-ratio (6.29).

Figure 7.3 shows the species scores for the first two CANOCO axes with the environmental variables, including stock grazing, displayed as vectors for the 1997 Porton Down data. Species scores are very similar to those of the1997 ordination without grazing as an environmental vector (Figure 7.2). The biplot position for stock grazing appears at first to be slightly contradictory as it lies quite close to those of sward height and MG1 community. This would suggest therefore that the mostly winter grazing regime was having a relatively minor effect on the ranker areas of grassland which have been exclusively selected for this management and the ordination is not greatly affected by transects which are included in these areas.

Table 7.3: Results of CANOCO analysis of the Porton Down 1997 transect data (including stock grazing as an environmental variable)

	Axis			
	1	2	3	4
Eigenvalue	0.149	0.075	0.049	0.04
Species-env. correlations	0.849	0.739	0.694	0.661
Cumulative percentage variance				
of species data	11.0	16.5	20.1	23.0
of species-env. relation	34.1	51.3	62.5	71.6
Interset correlations of environmental variables with axes (Rank):				
Sward Height	0.606 (3)	0.355	0.810 (2)	-0.232
Rabbit Index	0.680 (=2)	-0.439	-0.261	0.275
Slope	0.600	0.190	0.780 (3)	0.350
Aspect	-0.820 (1)	0.500 (=3)	-0.272	-0.151
Scrub	-0.134	0.950 (1)	-0.378	0.246
Bare	-0.238	-0.329	-0.173	0.820 (1)
Stones	-0.258	-0.177	-0.149	0.300
Stock Grazing	0.507	-0.231	0.103	0.257
CG2	-0.298	-0.840 (2)	-0.930 (1)	0.193
CG3	-0.200	0.160	-0.620 (4)	-0.183
CG6	0.144	-0.170	-0.520	-0.217
CG7	-0.186	-0.300	0.364	0.780 (2)
MG1	0.442	0.413	0.600	-0.400 (4)
MG5/6	0.680 (=2)	0.500 (=3)	0.330	-0.580 (3)

7.3 FRAGMENTED SITES LOCAL SCALE DATA

Table 7.4 shows the results of a CANOCO analysis of the Fragmented Sites transect (local scale) data for 1996 only.

The first axis accounted for 35.3 percent of the species-environment relationship while the second axis accounted for a further 16.3 percent. However, an unrestricted Monte Carlo test was carried out on axis 1 and was significant at $P = 0.01$ with a fairly high F-ratio (8.78). Calculated inflation factors showed that correlations among environmental variables was not a problem in this analysis (all inflation factors < 4.0).

Figure 7.3: CANOCO plot of first two axes showing ordination of Porton Down 1997 local scale data omitting stock grazing as an environmental variable. Environmental vectors shown as arrows (length x2). CG3, MG5/6, aspect, slope, scrub not shown

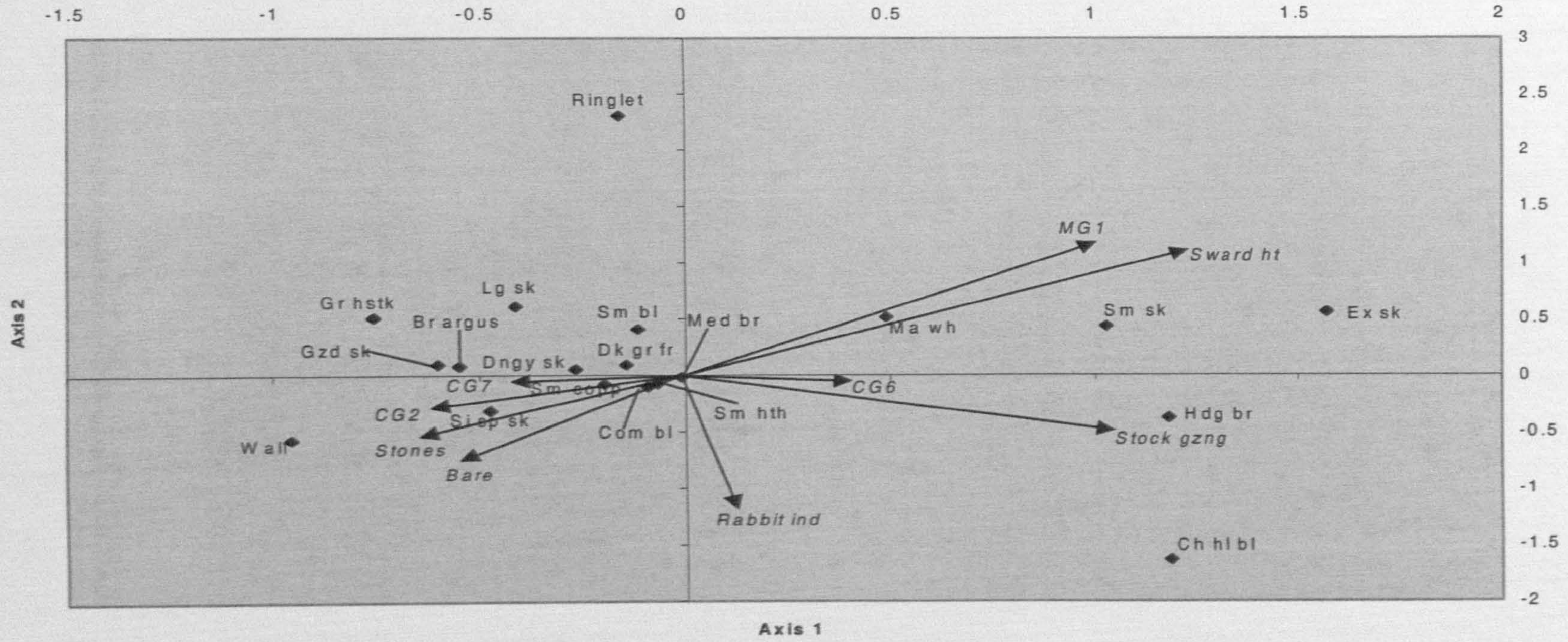


Table 7.4: Results of CANOCO analysis of the Fragmented Sites 1996 local scale data

	Axis			
	1	2	3	4
Eigenvalue	0.121	0.056	0.044	0.030
Species-env. correlations	0.827	0.716	0.709	0.604
Cumulative percentage variance				
of species data	10.1	14.8	18.5	21.0
of species-env. relation	35.3	51.6	64.5	73.3
Interset correlations of environmental variables with axes (Rank):				
Sward Height	0.604 (2)	0.228	-0.257	0.236
Rabbit Index	-0.175	-0.300	0.287	0.169
Slope	0.370	-0.289 (=4)	0.960 (1)	0.980 (1)
Aspect	-0.259	0.275	-0.351	-0.102
Scrub	0.272	-0.338 (2)	-0.268	0.170
Bare	-0.434 (4)	-0.396 (1)	-0.150	0.650 (1)
Stones	-0.411	-0.139	-0.148	0.111
Stock Grazing	-0.334	-0.297 (3)	-0.400 (4)	-0.270
CG2	-0.479 (3)	-0.156	0.212	0.118
CG3	-0.168	-0.192	-0.377	-0.840 (=3)
CG6	0.160	0.181	0.940 (2)	0.106
CG7	-0.229	-0.240	0.570 (3)	0.328
MG1	0.361	0.166	-0.171	-0.880 (2)
MG5/6	0.690 (1)	0.289 (=4)	0.350	-0.840 (=3)
W21/24	0.177	0.151	-0.255	0.680

Figure 7.4 shows the species scores for the first two CANOCO axes with the environmental variables displayed as vectors for the 1996 Fragmented Site data. Species were again grouped largely into the rank sward and larval grass-feeders at one end and those associated with well-grazed swards at the other end of the ordination.

The position of dark green fritillary shows no relation to habitat associations arising from the Porton Down local scale analyses. The reason for this is discussed in Section 7.5.

7.4 PORTON DOWN PATCH DATA

Table 7.5 shows the results of a CANOCO analysis of the Porton Down patch data for 1995 only.

The first axis accounted for 36.9 percent of the species-environment relationship while the second axis accounted for a further 14.8 percent. An unrestricted Monte Carlo test was carried out on axis 1 and was significant at $P = 0.01$ but with a fairly low F-ratio (4.49). Calculated inflation factors showed that correlations among environmental variables were generally higher in this analysis with sward height, average distance to nodes and distance to nearest node all > 5.0.

Inspection of Table 7.5 shows that axis 1 is correlated most strongly with the vectors sward height, MG1 and average distance to nodes in one direction and CG7 in the other. Axis 2 is correlated most strongly with the vectors MG5/6, CG7 and patch area in one direction and average distance to nodes in the other.

Figure 7.4: CANOCO plot of first two axes showing ordination of Fragmented Sites 1996 local scale data. Environmental vectors shown as arrows (length x2)

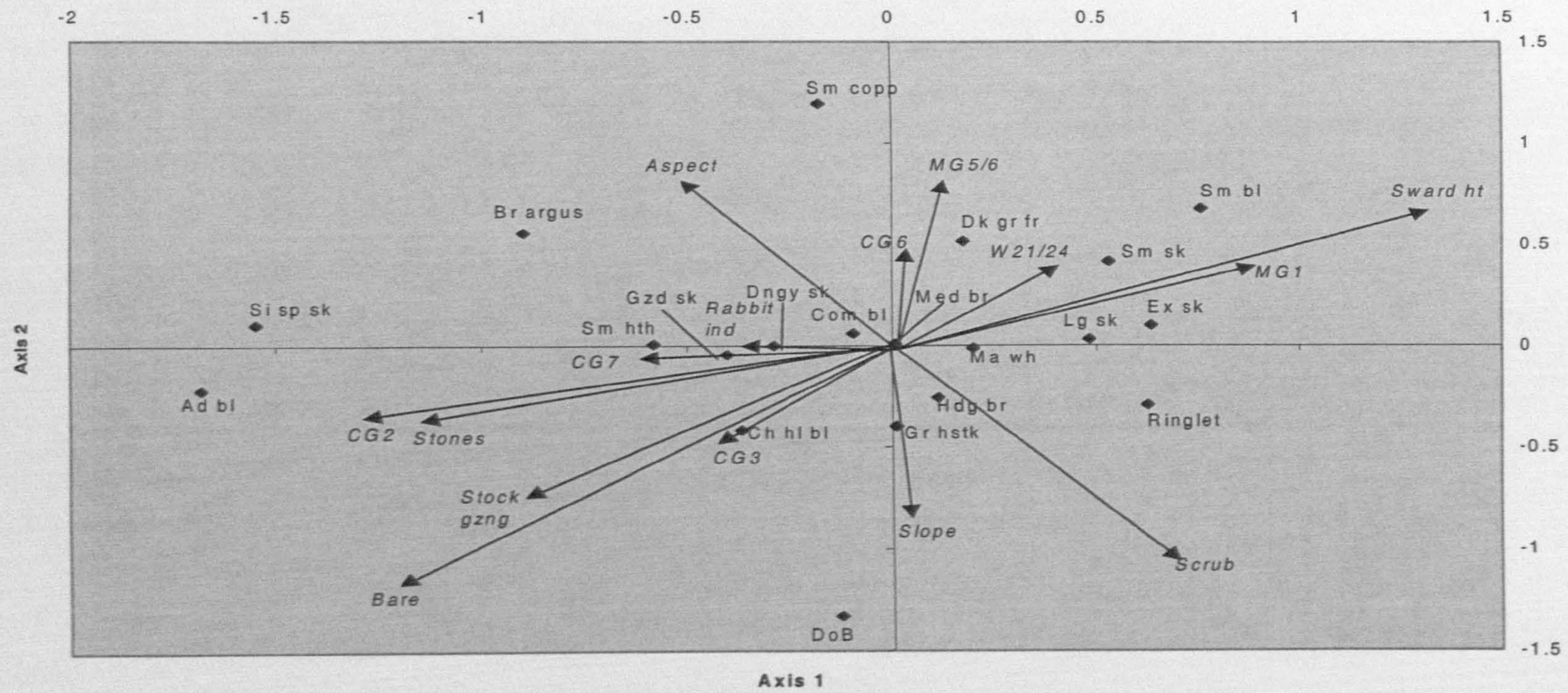


Table 7.5: Results of CANOCO analysis of the Porton Down 1995 patch data

	Axis			
	1	2	3	4
Eigenvalue	0.194	0.078	0.061	0.047
Species-env. correlations	0.939	0.854	0.843	0.842
Cumulative percentage variance				
of species data	24.3	34.1	41.6	47.5
of species-env. relation	36.9	51.7	63.2	72.1
Interset correlations of environmental variables with axes (Rank):				
Sward Height	0.462 (4)	0.068	0.212	0.176
Rabbit Index	-0.443	0.093	-0.061	-0.013
Slope	-0.112	-0.072	-0.056	0.363 (1)
Aspect	-0.125	-0.103	-0.164	-0.059
Scrub	0.195	-0.065	-0.205	-0.344 (2)
Bare	0.022	0.130	-0.409 (1)	-0.152
Stones	-0.092	0.172	-0.355 (3)	-0.276
CG2	0.097	0.127	-0.385 (2)	0.178
CG3	0.127	-0.218	-0.056	0.282 (4)
CG6	-0.045	-0.220	0.108	0.291 (3)
CG7	-0.520 (2)	0.356 (3)	-0.117	-0.064
MG1	0.550 (1)	0.041	0.115	-0.065
MG5/6	0.460	0.570 (1)	0.224	0.099
Nearest Node	0.425	-0.208	-0.180	0.234
Ave Dist Nodes	0.513 (3)	-0.257 (4)	-0.107	0.201
Patch Area	-0.344	0.534 (2)	0.304 (4)	-0.075

Species scores for the first two CANOCO axes with environmental variables displayed as vectors are shown in Figure 7.5. The only species which clearly shows a relationship with any landscape vectors is ringlet, which lies on the plane of both vectors related to distance to population nodes.

In order to investigate the importance of the landscape variables alone a further CANOCO analysis was performed with the three landscape variables only. The results are shown in Table 7.6.

The first axis accounted for 69.2 percent of the species-environment relationship while the second axis accounted for a further 21.5 percent. However, when an unrestricted Monte Carlo test was carried out on axis 1 it was not significant (P = 0.06). The eigenvalues of both axis 1 and 2 are also low and therefore only a limited amount of additional information is provided by this analysis.

Figure 7.5: CANOCO plot of first two axes showing ordination of Porton Down 1995 patch data. Environmental vectors shown as arrows (length x2). Bare and stones not shown

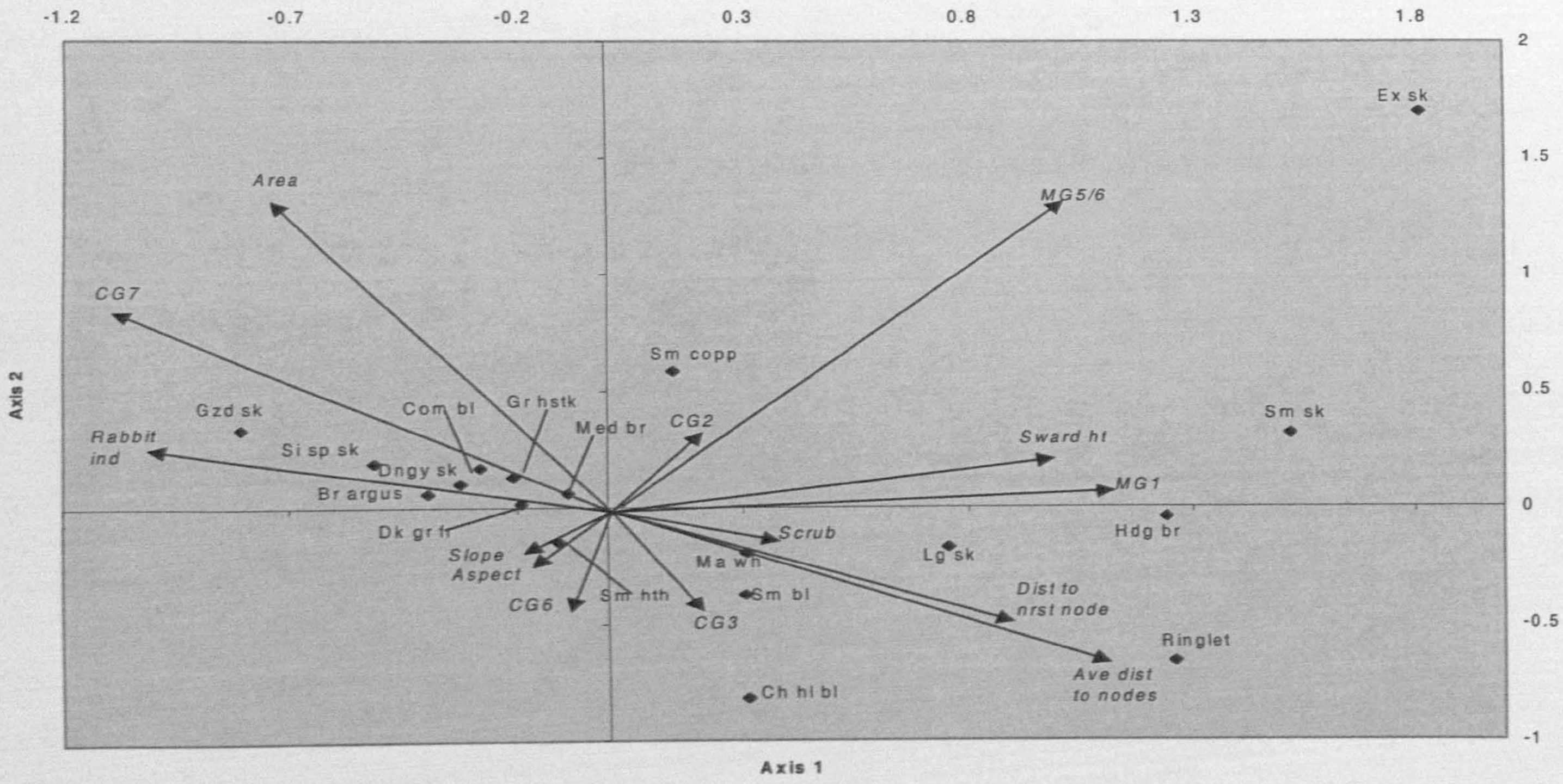


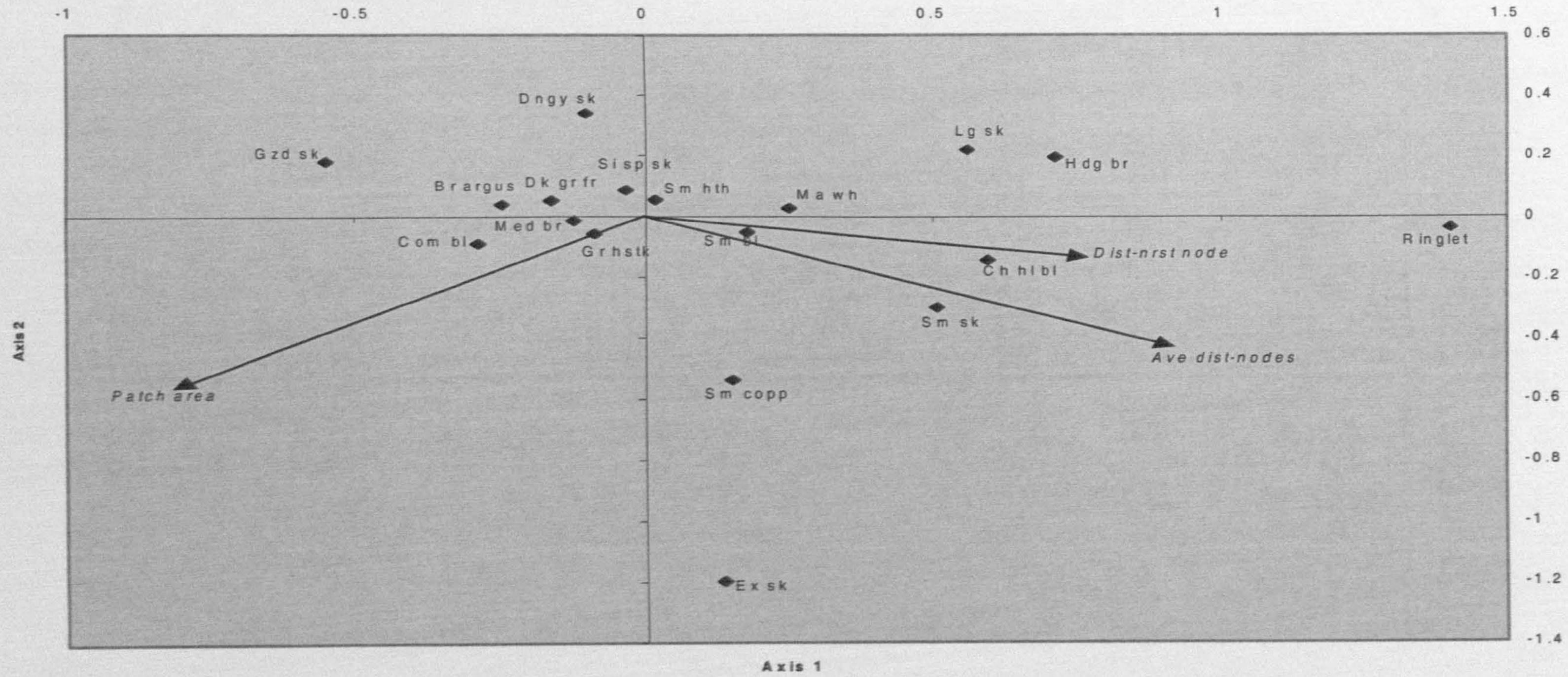
Table 7.6: Results of CANOCO analysis of the Porton Down 1995 patch data (landscape variables only)

	Axis			
	1	2	3	4
Eigenvalue	0.087	0.027	0.012	0.000
Species-env. correlations	0.715	0.560	0.450	0.000
Cumulative percentage variance				
of species data	10.9	14.3	15.7	0.0
of species-env. relation	69.2	90.7	100.0	0.0
Interset correlations of environmental variables with axes (Rank):				
Dist-Nrst Node	0.547 (3)	-0.089 (3)	0.281 (1)	0.000
Ave Dist Nodes	0.643 (1)	-0.227 (2)	0.075 (3)	0.000
Patch Area	-0.586 (2)	-0.296 (1)	0.100 (2)	0.000

The positions of some species on the ordination of species with local and landscape vectors shown in Figure 7.5 are exaggerated somewhat by this analysis as shown in Figure 7.6.

Ringlet is clearly related to greater distances from the grassland species nodes. This is due to the species being associated with rank grassland and tall scrub or woodland edge and its avoidance of open grassland where its microhabitat and food-plants would be too desiccated (BUTT 1986; Pollard and Yates 1993). This would also be true for hedge brown but to a lesser extent. The only other species which stands out somewhat along axis 1 and from the main cluster of species around the origins of the axes is grizzled skipper.

Figure 7.6: CANOCO plot of first two axes showing ordination of Porton Down 1995 patch data, landscape scale variables only. Environmental vectors shown as arrows (true scale)



7.5 FRAGMENTED SITES PATCH AND LANDSCAPE SCALE DATA

Table 7.7 shows the results of a CANOCO analysis of the Fragmented Sites patch data for 1996 and 1997 combined.

The first axis accounted for 29.0 percent of the species-environment relationship while the second axis accounted for a further 20.3 percent. Both axes are of a similar level of importance in explaining variation in the data therefore. An unrestricted Monte Carlo test was carried out on axis 1 and was significant at P = 0.01 but with a fairly low F-ratio (4.85). Calculated inflation factors showed that correlations among environmental variables were not a problem for all but two in this analysis (inflation factors for bare and stones 7.9 and 5.7 respectively, all the rest < 4.0).

Table 7.7: Results of CANOCO analysis of the Fragmented Sites patch data

	Axis			
	1	2	3	4
Eigenvalue	0.147	0.103	0.057	0.039
Species-env. correlations	0.901	0.852	0.781	0.698
Cumulative percentage variance				
of species data	12.2	20.7	25.5	28.7
of species-env. relation	29.0	49.3	60.6	68.3
Interset correlations of environmental variables with axes (Rank):				
Sward Height	-0.640 (1)	0.441 (3)	0.010	0.047
Rabbit Index	0.392	-0.113	-0.244	-0.014
Slope	0.052	-0.275	0.137	0.048
Aspect	0.209	0.416 (4)	0.218	0.030
Scrub	-0.593 (2)	-0.368	0.145	0.110
Bare	0.154	-0.479 (2)	0.465 (1)	0.088
Stones	0.113	-0.320	0.390 (2)	0.163
Stock Grazing	0.264	-0.162	0.163	-0.090
CG2	0.462 (4)	-0.343	0.090	0.057
CG3	-0.266	-0.073	0.365 (3)	-0.402 (2)
CG6	0.151	-0.130	-0.308 (4)	0.130
CG7	0.256	0.054	-0.185	0.004
MG1	-0.194	0.248	0.080	-0.438(1)
MG5/6	0.077	0.205	-0.191	-0.177
W21/24	-0.294	0.065	0.108	0.349 (3)
Distance-PD	-0.084	-0.518 (1)	-0.294	-0.198 (4)
Ave Dist Patches	0.284	-0.266	-0.274	-0.112
Patch Area	0.513 (3)	-0.070	0.077	-0.171

Figure 7.7 shows the species scores for the first two CANOCO axes with the environmental variables displayed as vectors for the 1996 and 1997 combined Fragmented Site patch data. Although the ordination has 'flipped' along the first axis (a common occurrence in ordination analysis), the species groupings are largely similar in comparison to the previous analysis at a local scale with one exception, the small blue. This species was only recorded on three transects over the two years (one in 1997) and therefore appears to show sensitivity to the analysis due to its inconsistency in terms of broad habitat selection. The wall occurred on one Fragmented Site in 1997 and strongly reflected the habitat selection displayed on Porton Down (see Section 7.2).

It was decided to investigate the importance of the landscape variables alone so a further CANOCO analysis was performed with the three landscape variables only. The results are shown in Table 7.8.

The first axis accounted for 57.5 percent of the species-environment relationship while the second axis accounted for a further 34.3 percent. Both axes are of a similar level of importance in explaining variation in the data as reflected in their eigenvalues. An unrestricted Monte Carlo test was carried out on axis 1 and was significant at $P = 0.01$ but with a fairly low F-ratio (3.92). Calculated inflation factors showed that correlations among environmental variables were not a problem in this analysis (all < 2.0).

Figure 7.7: CANOCO plot of first two axes showing ordination of Fragmented Site whole patch and landscape data. Environmental vectors shown as arrows (length x2)

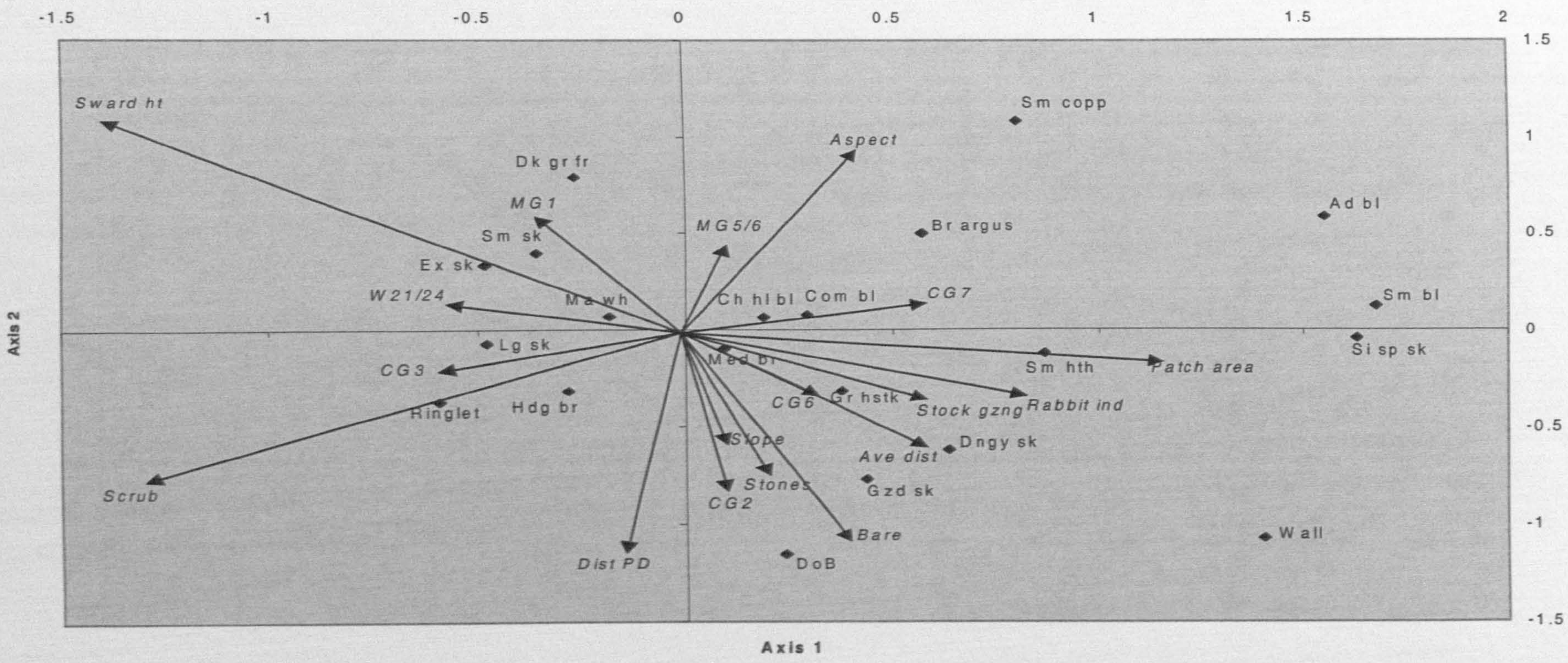
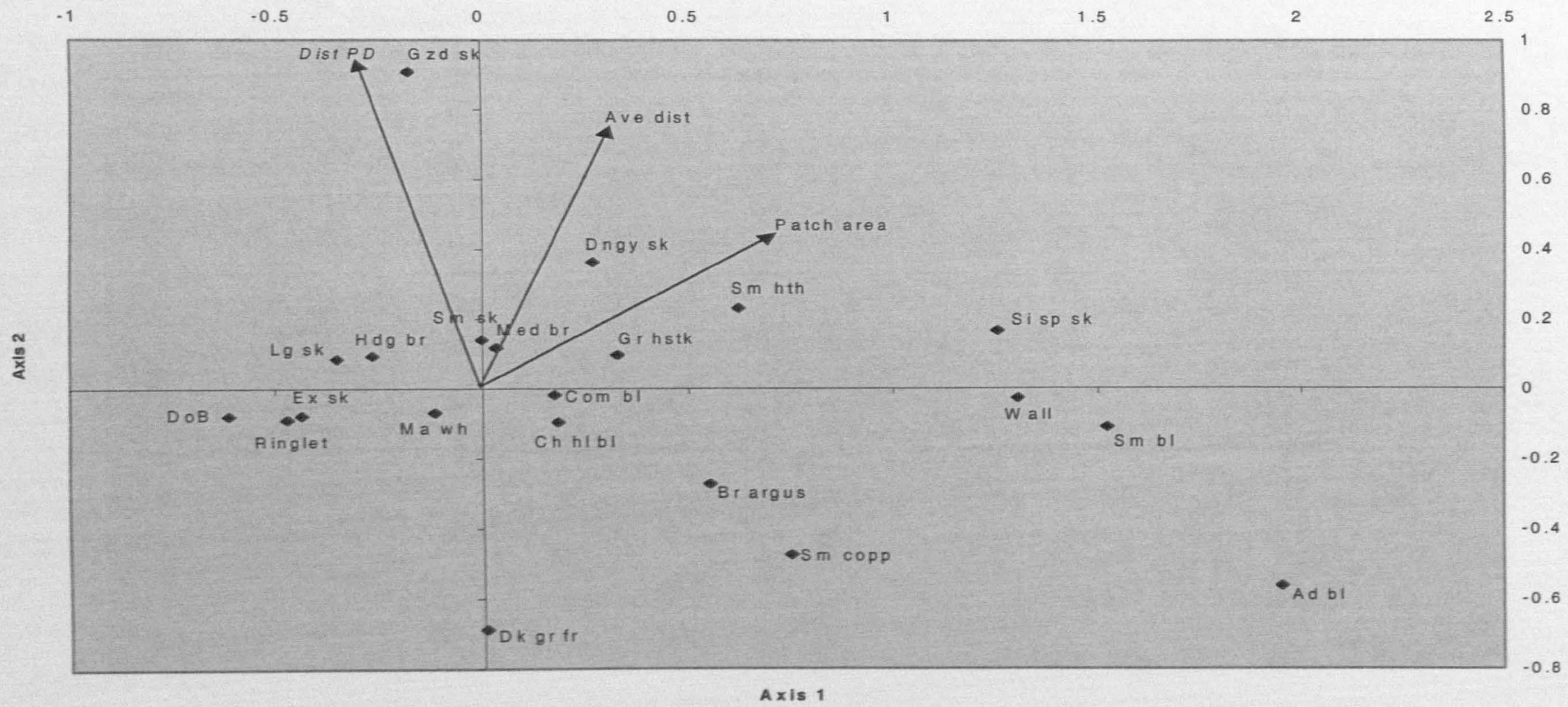


Table 7.8: Results of CANOCO analysis of the Fragmented Sites patch data for 1996 and 1997 combined (landscape variables only)

	Axis			
	1	2	3	4
Eigenvalue	0.088	0.053	0.013	0.000
Species-env. correlations	0.711	0.66	0.445	0.000
Cumulative percentage variance				
of species data	7.3	11.6	12.7	0.0
of species-env. relation	57.5	91.8	100.0	0.0
Interset correlations of environmental variables with axes (Rank):				
Distance-PD	-0.234 (2)	0.621 (1)	0.031 (3)	0.000
Ave Dist Patches	0.200 (3)	0.501 (2)	-0.261 (1)	0.000
Patch Area	0.500 (1)	0.283 (3)	0.252 (2)	0.000

Figure 7.8 shows the species scores for the first two CANOCO axes with the environmental variables distance to Porton Down, average inter-patch distance and patch area only displayed as vectors for the 1996 and 1997 combined Fragmented Site patch data. As shown by the inter-set correlations of environmental variables with axes in Table 7.8 above, axis 1 separates species according to their affinity with patch area while axis 2 separates species according to their affinity with the 'connectivity and distance' variables.

Figure 7.8: CANOCO plot of first two axes showing ordination of Fragmented Site whole patch data, landscape scale variables only. Landscape vectors are shown (true scale)



The ordination plot is very revealing in that most species are spread only along axis 1, with adonis blue, small blue, silver-spotted skipper and wall appearing to require large patches.

There are four species which appear to show sensitivity to the distance vectors as they show some 'spread' along axis 2. However, any species showing a relationship along the positive part of this axis can only be doing so due to a chance location of (a) strong population(s) on sites away from Porton Down as any real effect would be a negative one. Inspection of the raw data for Fragmented Sites reveals that the two strongest colonies of grizzled skipper outside Porton Down were at site Ee (Broughton Down, 3.5km distant) and site Ll-Oo (RNAD Dean Hill, 9km distant) where the highest counts occurred (see Table 2.1). This explains this species' position on the second axis close to the 'distance from Porton Down' vector.

7.6 DISCUSSION

From the analysis of Porton Down 1995 local scale data (Table 7.1 and Figure 7.1), the positions of the species reflect the environmental variables shown to be important in the GLIM analyses (see Chapter 4). The group of seven larval grass-feeders on the positive side of axis 1 are related to ranker, taller grass-dominated plant communites, although the ubiquitous meadow brown shows no affinity. The position of the ringlet also reflects its negative relationship with warm, sunny aspects (Section 4.25). Conversely, adonis blue shows the well known affinity to hot south-facing, well-grazed slopes (Thomas 1983a). The group of species in the top left quadrant of the ordination is generally related to open swards, well grazed by rabbits (and therefore with much bare ground and dug-up flints and

chalk pieces – the environmental variable 'stones'). These are the conditions under which the two NVC communities CG2 and CG7 are maintained (Rodwell 1992). All of the species in this quadrant have major larval food-plants associated with one or both of these communities (Rodwell 1992).

The position of small blue is interesting as the GLIM analysis was unable to explain the species' presence (Section 4.12). This species is known to be intolerant of anything but moderate grazing pressure as the eggs and larvae are very vulnerable due to locating themselves on the flower heads (BUTT 1986; Coulthard 1982). It also likes some scrub and warm, sunny aspects. Its larval food-plant *Anthyllis vulneraria*, is frequent in all CG communities but CG6 (Rodwell 1992), and so its position on the ordination appears to reflect the lack of grazing plus aspect and scrub presence.

Comparisons of the Porton Down 1995 local scale and Fragmented Site local scale analyses (Tables 7.1 to 7.4 and Figures 7.1 to 7.4), show many similarities. One species which was common enough to include in the Fragmented Site local scale analysis, Duke of Burgundy, is located along axis 2 which is related to the presence of scrub, bare ground, stock grazing and slope. This reflects the peculiarity of the sites where it was found, two of which were scarps, lightly grazed by sheep and Icelandic horses and the other a bank alongside a droveway. All sites had stock- or footpaths along them (hence the association with 'bare ground'). These sites fit well with the known requirements of this species for warm micro-habitats, usually at the scrub-grassland interface where its food-plants *Primula veris* and *P. vulgaris* are sheltered and therefore large-leaved (Oates 2000; BUTT 1986).

The positions of some other species are also clear in a management context. For example, chalkhill blue appears to thrive under a moderate stock grazed regime among broken ground while adonis blue and silver-spotted skipper prefer the harder grazed sunnier slopes. Small copper here shows an association with NVC types MG5/6, where its chalk grassland food-plant, *Rumex acetosa* is commonly found, particularly on the sub-community MG5a which is often associated with horse-grazing (Gibson 1995).

In reference to the Porton Down Patch analysis (Section 7.4), the GLIM analyses in Chapter 5 showed that five species had significant negative relationships with distances to population nodes (plus one near-significant). However, only one, grizzled skipper, appears to show this relationship on the ordination plot. This implies that these landscape variables are not of over-riding importance in comparison to the local scale variables. The negative relationship of small heath with patch area shown in the GLIM analysis is partly reflected in the species' position on the ordination but appears to be more influenced by the other variable selected in GLIM (aspect). The position of grizzled skipper also re-iterates the GLIM patch analysis where a negative relationship with distance to the nearest population node was the only significant variable.

The positions of small copper and Essex skipper on axis 2 are also clearly influenced by patch area which ranked second in the previous analysis and first in this. This is probably due to the rarity of their habitat at Porton Down which has been shown to be towards the MG1 to MG5/6 NVC communities in the previous analyses. The larger patches are more likely to have patches of these rare communities within them or at their edges, often on tracksides.

The Fragmented Sites landscape scale ordination explains the anomalous position of dark green fritillary in the Fragmented Site local scale analysis (Section 7.3). GLIM analysis showed that despite strong affinities with the presence of the CG3 community and its food-plant *Viola hirta* shown by local scale analysis of Porton Down populations (see Chapter 4), the presence of this species on Fragmented Sites was over-ridingly determined by a combination of distance from Porton Down and the average distance between patches. This is almost precisely reflected by the position of dark green fritillary as a negative product of these two vectors on the ordination diagram (Figure 7.7).

Five species showed a relationship with patch area in the GLIM analyses, although they all showed additional relationships with local scale variables. Three species, small heath, green hairstreak and dingy skipper are all positioned on or close to the patch area vector, their closeness reflecting the relative importance of this variable (see Chapter 6).

Large skipper showed a relationship with patch area in the GLIM analysis that was the result of a correlation product with the CG3 community and this is reflected by its position close to this vector on the ordination (Figure 7.7).

The only apparently anomalous species among this group is small skipper. The GLIM analyses, both at a local scale on Porton Down and on Fragmented Sites, showed a strong affinity to long grass and no rabbit grazing. This species is known to favour grassy edges, along paths and tracks for example (BUTT 1986), and these micro-habitats are relatively scarce on the generally widely grazed chalk grassland sites in this study. The relationship with patch area in the GLIM analysis is almost certainly an artefact of the increasing probability of a minimum number of suitable habitat patches with an increase in whole

patch area. This single variable is therefore masked by the combined relative importance of the other local scale variables in the ordination.

When only landscape scale variables were included in the ordination analysis, the position of dark green fritillary confirmed the findings of the previous CANOCO analysis and the GLIM analysis that the two distance vectors are very important in determining the species' presence at Fragmented Sites. Another species, adonis blue, was only present in strong numbers at one site, Figsbury Ring, (site I), which, although within 1km of Porton Down, presents almost ideal habitat conditions for the species due to careful stock grazing management and hot, sunny aspects on the steep slopes of the iron age fortifications. It is unlikely that Porton Down has ever been a major source population for replenishing this local population as numbers of the major colony within Porton Down, on Thorneydown, have never been high since the 1950s (R Ryan pers. comm.). Metapopulation processes may nevertheless be acting between these two local populations and the only other potentially viable one at Cockey Down, (site O), 3km from Porton Down and less than 2km from Figsbury Ring.

The position of one of the two remaining species which appear to be influenced by the 'distance' vectors along axis 2 was confirmed by the GLIM analyses. Brown argus showed quite a strong but insignificant effect of the average distance between sites in a logistic regression analysis ($\chi^2_1 = 3.483$; $P > 0.05$). For small copper, distance from Porton Down was the next ranked variable in the GLIM logistic analysis, but did not approach significance.

Overall, these analyses at the community level have reiterated and to a degree, simplified the GLIM analyses. The capability of CANOCO to include species with low frequencies, which inevitably tend to be the rarer ones (both regionally and nationally), is also useful as these species often show extremes in terms of habitat selection (Oates 1995). Positions of such species in ordination space can therefore help place more generalist species in context. The major finding, however, is that most species show a mixed reaction to a combination of resources at a local scale and landscape scale factors which are known to determine long-term survival of populations and metapopulations (Hanski 1999). The link between patch area and resource availability, implicit in metapopulation ecology (Hanski 1999), is also pointed at by several species in both the GLIM and community analyses. The effect of distance, presumably on dispersal between colonies and populations, is however, a relatively unimportant factor, at least in this study system.

8. INCIDENCE FUNCTION MODELS

8.1 INTRODUCTION

This chapter examines modelled metapopulation parameters (relating to minimum patch area, degree of environmental stochasticity, colonization ability and the effect of distance on dispersal) and compares these to the landscape level model parameters arising from GLIM regression analyses (see Section 2.7). Seven species qualified for Incidence Function Model (IFM) modelling under the criteria in Hanski (1994) (see Section 2.7) from the Fragmented Sites. These were grizzled skipper, dingy skipper, green hairstreak, small copper, brown argus, chalkhill blue and dark green fritillary.

The model parameters and their meaning can be summarized as follows:

e and x are parameters of annual extinction probability E as a function of patch area $E = e/A^x$.

x reflects the effective strength of environmental stochasticity and the value decreases with increasing environmental stochasticity.

y describes the colonization ability of a species. Good colonizers, which are little affected by isolation, have small y values.

- α is the effect of distance on dispersal. The quicker the drop-off in a species' dispersal ability, the greater the value.

A_0 is the critical minimum patch area where extinction probability in unit time is 1.

The following is an approximate guide to values used where some parameters are not themselves modelled:

For α, values are usually set at -0.5 for the most dispersive species, -1.0 for moderately dispersive species, -2.0 for intermediate and -3.0 for the most sedentary species. All values from R. Wilson, Leeds University pers. comm.

x is usually set at 1.0, which is considered to be an average value for all species (A. Moilanen pers. comm.).

8.2 RESULTS

Means (±1 standard error) of parameter estimates are shown in Table 8.1.

8.3 LINKING IFM AND INDEPENDENT ANALYSES

8.3.1 Population Variability and Critical Minimum Patch Area (A_0)

The relationship between population variability (coefficient of variation of natural logarithm of values from Porton Down BMS 1994-99) and A_0 as modelled with the IFM is shown in Figure 8.1. This relationship is highly significant (Spearman Rank Correlation Coefficient, $r_s = 0.964$; $n = 7$, $P = 0.005$). BMS data from Porton Down were used as these local populations would show variation due to local scale environmental stochasticity and

these would be 'background' values. This innate population variability could be due to density-dependence (Hanski and Woiwod 1993) or more simply a result of local scale habitat selection which, if it results in reduced habitat heterogeneity, translates to a need for a larger patch area the more susceptible the species (Kindvall 1996).

Table 8.1: Means *(±1 standard error)* of parameter estimates

	Parameter				
Species	α	x	γ	e	A_0
Dingy skipper	-1.786	1.412	62.413	0.009	0.032
Erynnis tages	*(0.096)*	*(0.089)*	*(13.925)*	*(0.002)*	*(0.004)*
Grizzled skipper	-1.818	1.576	73.308	0.010	0.048
Pyrgus malvae	*(0.137)*	*(0.072)*	*(14.580)*	*(0.003)*	*(0.007)*
Green hairstreak	-1.220	1.347	31.081	0.035	0.084
Callophrys rubi	*(0.071)*	*(0.052)*	*(1.528)*	*(0.003)*	*(0.009)*
Brown argus	-0.870	1.319	57.06	0.0195	0.050
Aricia agestis	*(0.035)*	*(0.057)*	*(4.154)*	*(0.002)*	*(0.006)*
Chalkhill blue	-0.945	1.161	32.947	0.025	0.042
Lysandra coridon	*(0.039)*	*(0.042)*	*(1.416)*	*(0.002)*	*(0.005)*
Dark green fritillary	-1.217	0.763	12.924	0.0198	0.006
Argynnis arglaja	*(0.101)*	*(0.023)*	*(1.393)*	*(0.001)*	*(0.001)*
Small heath	-1.107	1.471	111.765	0.0049	0.0255
Coenonympha pamphilus	*(0.047)*	*(0.047)*	*(14.093)*	*(0.001)*	*(0.003)*

One of the few species included in this study which has had independent estimates of A_0 is silver-spotted skipper. Thomas, Lewis and Hill (unpublished but shown in Thomas and Hanski 1997) estimated A_0 as ~0.5 ha from observational data. Hanski (1994), however, used Thomas' data to parameterize A_0 using an early version of the IFM and estimated the value at 0.0104 ha, with an observed value at 0.02 ha. Using a linear regression model applied to the data shown in Figure 8.1, $y = 0.001 + 0.294x$, the coefficient of variation for the silver-spotted skipper data from the Porton Down BMS (0.163), gives a predicted A_0 of 0.0489 for the entire patch network. This is close to the values estimated for the species associated with well-grazed chalk grassland such as grizzled skipper, and is not far from Hanski's estimate.

8.3.2 Parameter Estimates and their Relationship with Multivariate Analyses of Butterfly Species and Local and Landscape Scale Variables

The relationship between estimates for the parameter for effective strength of environmental stochasticity (x) and species' scores on CANOCO axis 1 of the Fragmented Site analysis is shown in Figure 8.2. The correlation is not significant (Spearman Rank Correlation Coefficient, $r_s = 0.714$; $n = 7$, $P = 0.1$). There is a trend however and the correlation would be reduced by the position of grizzled skipper. The linear regression model fitted to these data ($y = 1.038 + 0.637x$) gives a predicted value for the silver-spotted skipper parameter x at 2.077, given a CANOCO axis 1 score of 1.631 for this species. This is way beyond the estimates for the other species given in Table 8.1. It is possible that the relationship is non-linear and, fitting a second order polynomial to the data ($y = 1.068 + 1.008x - 0.656x^2$) gives a predicted value for the silver-spotted skipper

parameter x at 0.967, given a CANOCO axis 1 score of 1.631. This is remarkably close to the figure modelled by Hanski (1994) which was 1.009 (standard error 0.222).

Figure 8.1: The relationship between population variability (coefficient of variation of natural logarithm of values from Porton Down BMS 1994-99) and A_0

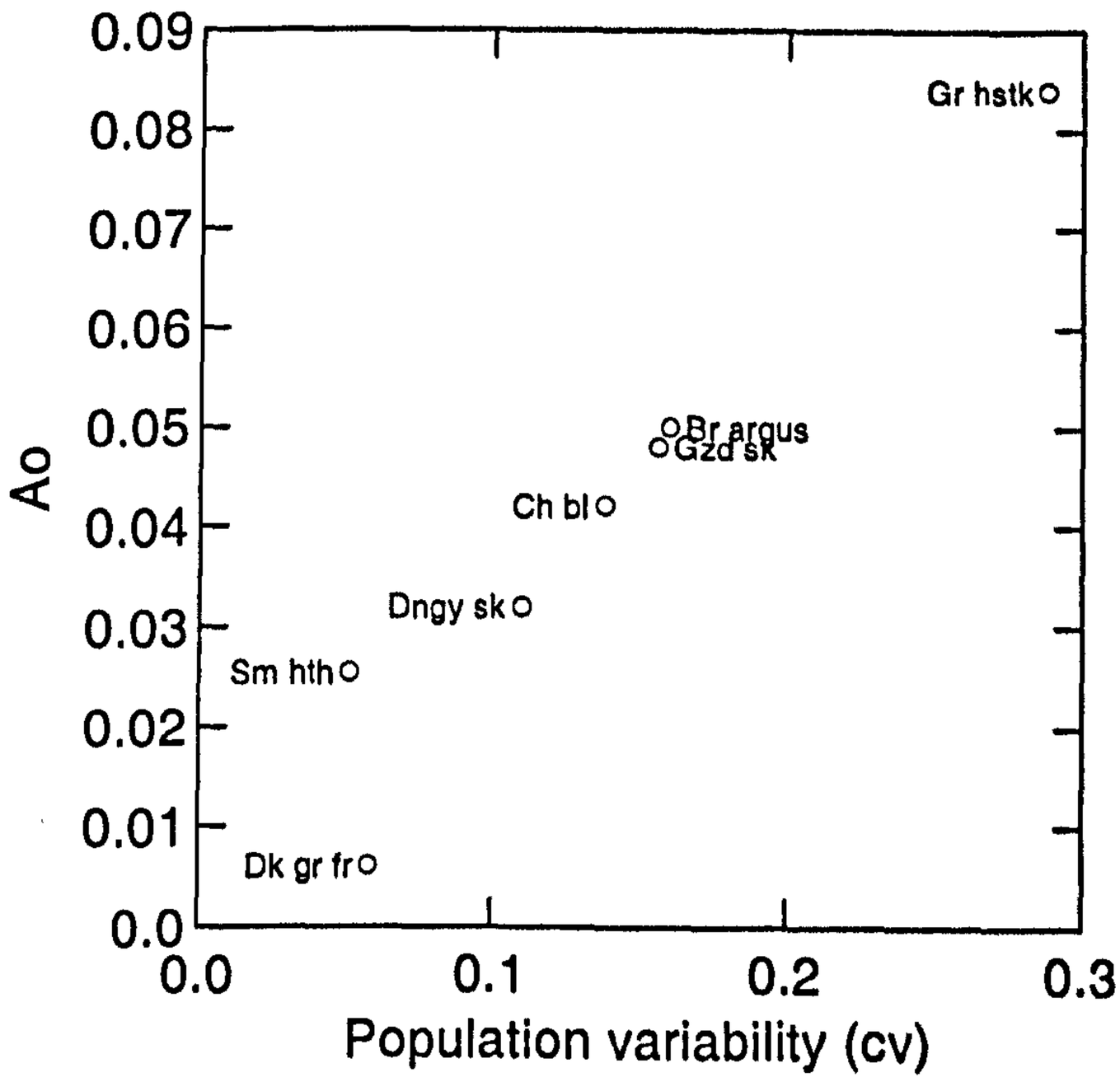
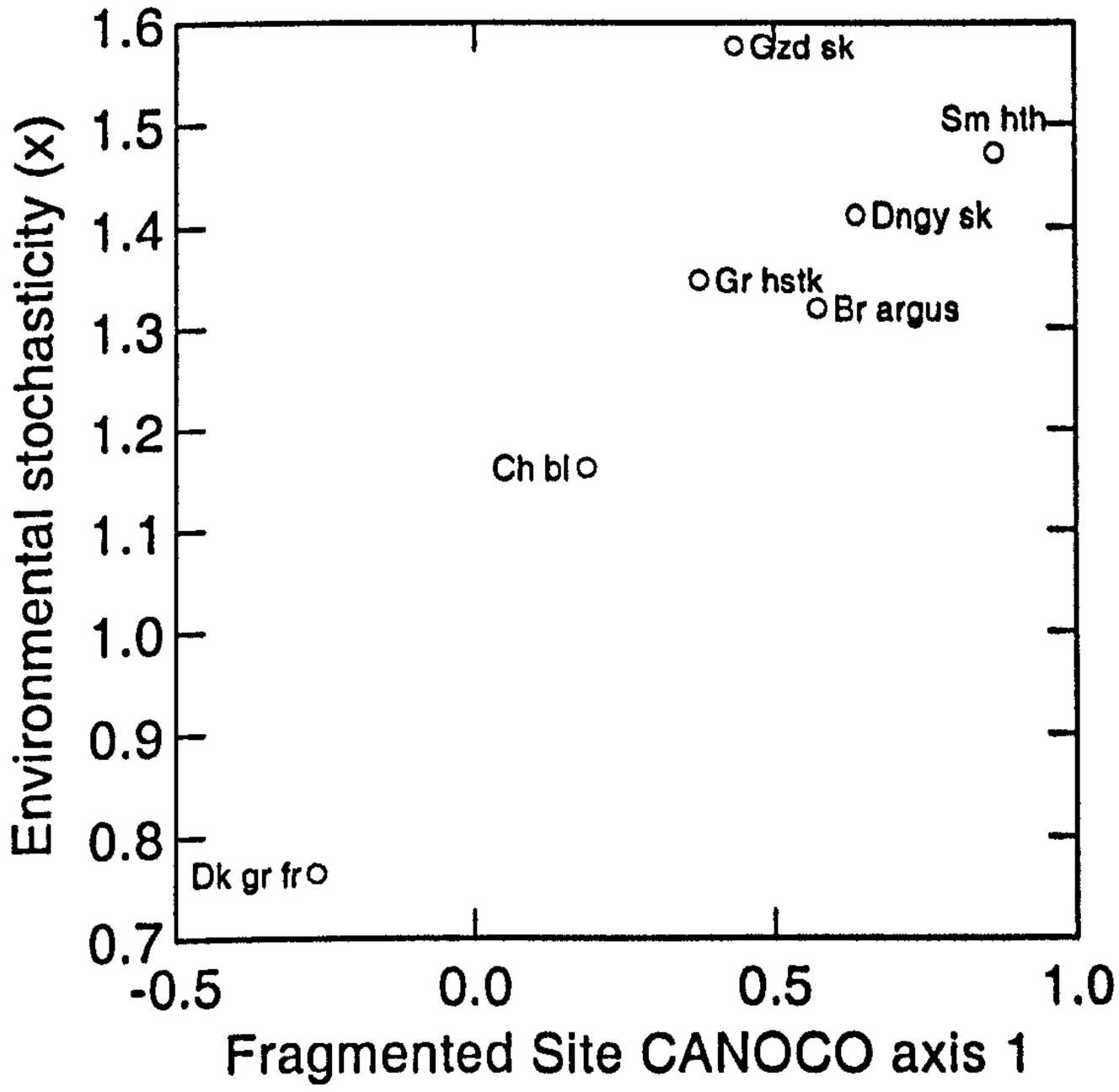
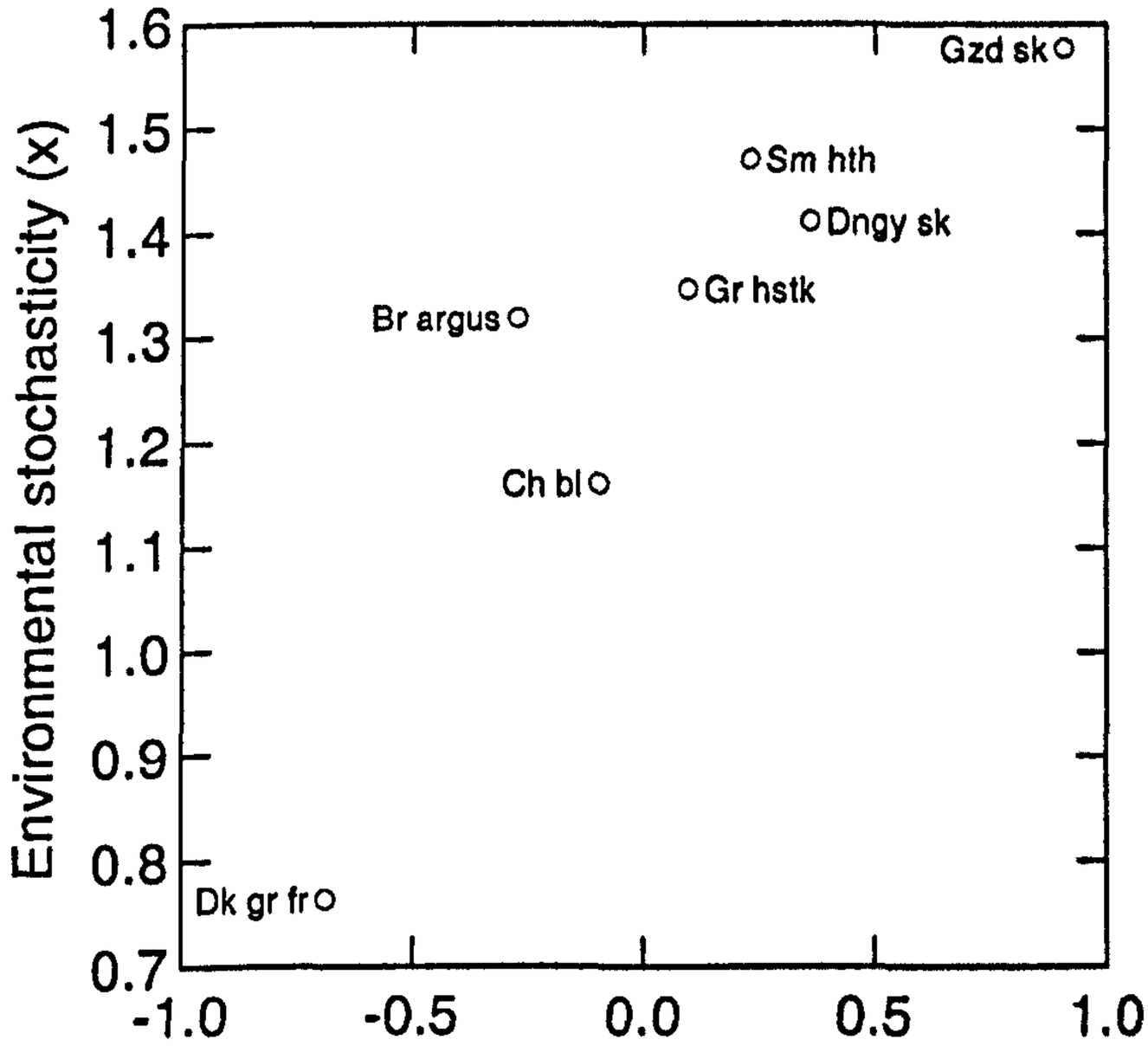


Figure 8.2: The relationship between the parameter for effective strength of environmental stochasticity (x) and species' scores on CANOCO axis 1 of the Fragmented Site analysis



The relationship between estimates for the parameter for effective strength of environmental stochasticity (x) and species' scores on CANOCO axis 2 of the Fragmented Site landscape variables analysis is shown in Figure 8.3.

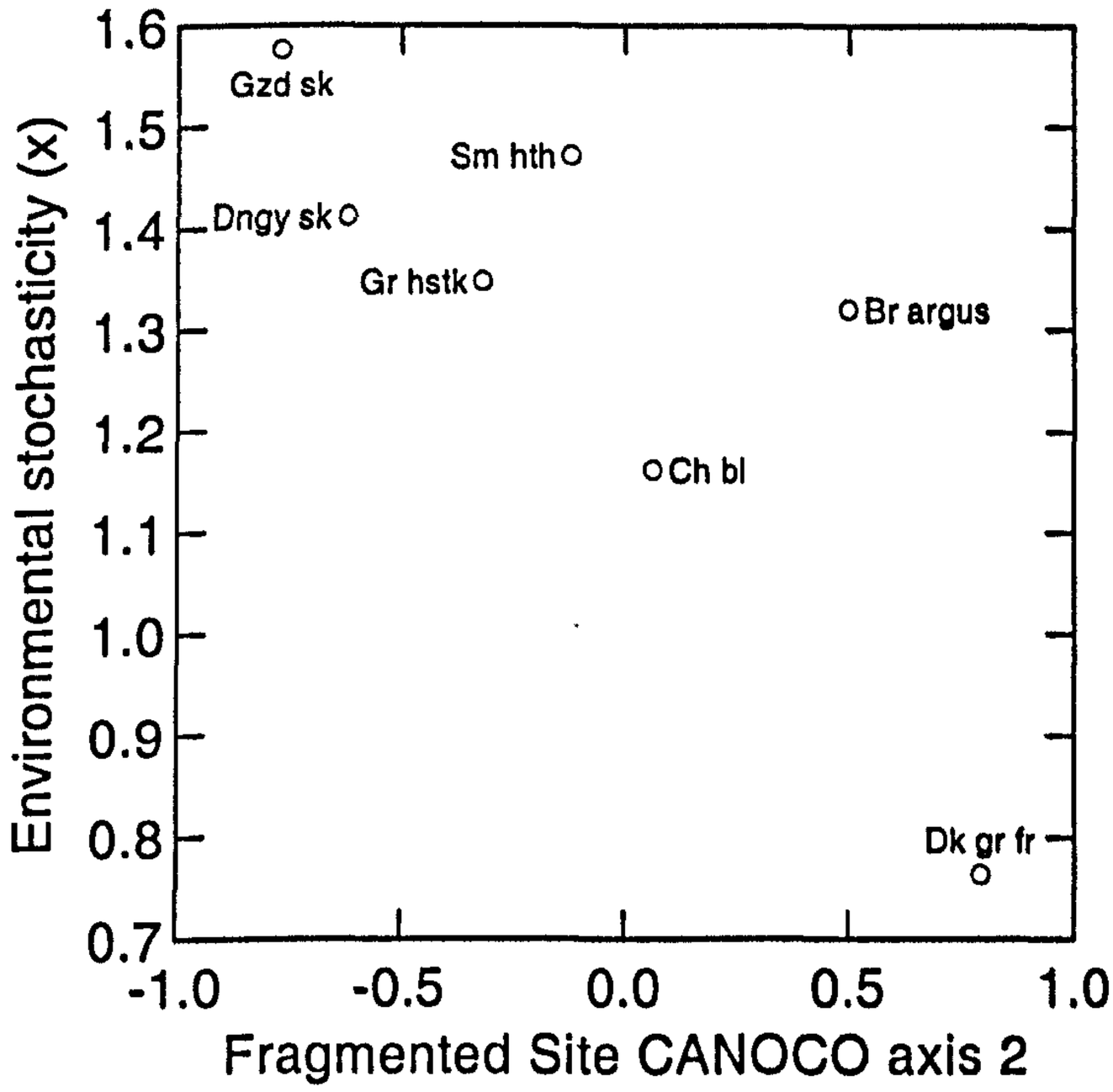
Figure 8.3: The relationship between the parameter for effective strength of environmental stochasticity (x) and species' scores on CANOCO axis 2 of the Fragmented Site landscape variables analysis



The correlation is significant (Spearman Rank Correlation Coefficient, $r_s = 0.929$; $n = 7$, $P = 0.01$). The linear regression model fitted to these data ($y = 1.256 + 0.467x$) gives a predicted value for the silver-spotted skipper parameter x at 1.334, given a CANOCO axis 2 score of 0.1667 for this species. This predicted value is even closer to Hanski's (1994) predicted value of 1.009 than that from the previous analysis. This shows that for this parameter at least, the landscape scale metapopulation dynamics have a strong influence and it is probable that the rescue effect (Brown and Kodric-Brown 1977, and Section 1.5), is a function mainly of the distances from Porton Down and between Fragmented Patches.

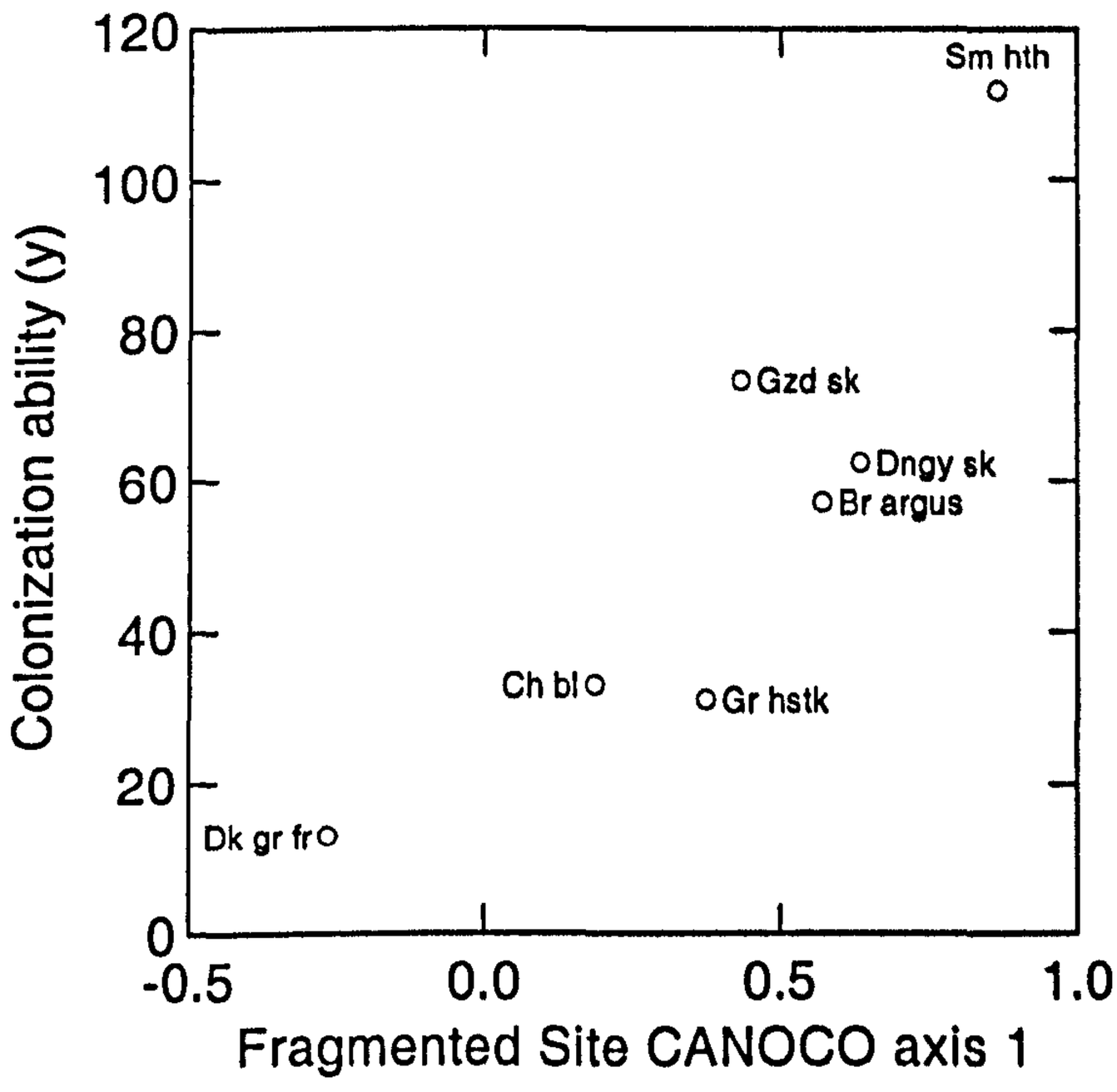
The relationship between estimates for the parameter for effective strength of environmental stochasticity (x) and species' scores on CANOCO axis 2 of the Fragmented Site analysis is shown in Figure 8.4. The correlation is significant (Spearman Rank Correlation Coefficient, $r_s = -0.857$; $n = 7$, $P < 0.05$). The linear regression model fitted to these data ($y = 1.267 - 0.384x$) gives a predicted value for the silver-spotted skipper parameter x at 1.284, given a CANOCO axis 2 score of -0.043 for this species. This axis also appears to predict the silver-spotted skipper score with a good level of accuracy despite its strong correlation with local scale variables as well as distance from Porton Down (Section 7.5). However, this axis had a relatively high eigenvalue and showed a much stronger correlation with distance from Porton Down than did axis 1 of the ordination (Section 7.5).

Figure 8.4: The relationship between the parameter for effective strength of environmental stochasticity (x) and species' scores on CANOCO axis 2 of the Fragmented Site analysis



The relationship between estimates for the parameter for the colonization ability of species (y) and species' scores on CANOCO axis 1 of the Fragmented Site analysis is shown in Figure 8.5. The correlation is significant (Spearman Rank Correlation Coefficient, r_s = 0.857; n = 7, $P < 0.05$). Good colonizers appear to lie at the negative end of axis 1 which is related to local scale variables. However, the positive end is related strongly to patch area and, to a lesser degree, distance between patches (ranked seventh of the eighteen variables), both of which would become more important to species with lower colonization ability.

Figure 8.5: The relationship between the parameter for the colonization ability of species (*y*) and species' scores on CANOCO axis 1 of the Fragmented Site analysis



Clearly, the apparent lack of relationship between good colonizers and landscape scale variables is a function of the small effect features such as patch size and inter-patch distance has on these species rather than a negative effect *per se*.

There were no significant relationships between IFM parameter estimates and species' CANOCO scores for the Porton Down patch data.

8.4 DISCUSSION

8.4.1 IFM Parameter Estimates

Dingy skipper appears to be a poor disperser over distance and a poor colonizer but is not badly affected by environmental stochasticity. The latter property is probably related to the species' flexibility of use of two larval food-plants, *Lotus corniculatus* and *Hippocrepis comosa*, both of which can be fairly abundant in some years and among different types of chalk grassland. All of the GLIM analyses found food-plant abundance to be a consistently significant factor in determining this species' presence. There is probably a relationship therefore, between this factor and the species' poor dispersal and colonization ability. Its habitat and food-plant requirements have historically been fulfilled across the chalk landscape and therefore local and regional extinction probabilities have been relatively low. Recent declines have been shown to be significant over both woodland and chalk grassland sites (Greatorex-Davies and Roy 2000). This may well be due to the landscape reaching a critically high degree of fragmentation (see Section 1.7).

Grizzled skipper has the highest values of all the species modelled for the effect of distance on dispersal and the effect of environmental stochasticity. It is also a poor colonizer. Marking studies have shown the species to have low mobility (Brereton 1997). Taken together, these factors would appear to make this species particularly vulnerable to local and regional extinctions. Indeed, the grizzled skipper has recently shown rapid declines in distribution and colony size over its British range (Brereton, Bourn and Warren 1998), although how much of this can be apportionately attributed to fragmentation and within-patch declines in habitat quality is not known. It is clear from the GLIM analyses

that high quality CG2 and/or CG7 grassland is preferred and this is at a premium in most regions now.

Green hairstreak has mid-range values for most parameters except the critical minimum patch area, which is the highest. This species is fairly conservative in its food-plant and structural habitat requirements, but the combination of deep soils (for scrub growth) and skeletal soils (for the food-plants) required to provide these (BUTT 1986) is actually an uncommon combination in any but the larger chalk downland patches. This would explain the relatively high A_0 value.

Brown argus also has mid-range values for most parameters except the effect of distance on dispersal which is the lowest. This should mean that the species has good powers of dispersal over a relatively high proportion of the inter-patch distances in the network. Despite worries over fragmentation of chalk grasslands, this species has not only maintained its populations on established colonies, but has (re-)colonized many sites following high population levels in 1995 and 1996 (Greatorex-Davies 1999; Fuller 1999). This reflects the strong value for the distance-dispersal parameter in the IFM model above and is reinforced by the consistent selection of local scale variables only in the GLIM analyses.

Chalkhill blue also shows a low value for the effect of distance on dispersal but with a relatively small value for the effect of environmental stochasticity. This species is renowned for huge, asynchronous population fluctuations at some colonies (annual indices of between 0 and 150 at Aston Rowant South in successive years for example, Greatorex-Davies and Roy (2000). The sole larval food-plant, *Hippocrepis comosa*, often remains

abundant during these fluctuations and it may therefore be due to this species' reliance on ants (*Lasius alienus, L. flavus* and *Myrmica sabuleti*) to tend the larvae and a possible sensitivity to timing of grazing which may cause high rates of over-wintering egg mortality. This combination of parameter values appears to give rise to similar circumstances to that of the marsh fritillary *Euphydryas aurinia*, which is known to rely on regular re-colonization from nearby patches within the metapopulation following near- or actual local extinction (Warren and Brereton 1998).

Dark green fritillary shows by far the smallest values for the effect of environmental stochasticity, colonization ability and minimum critical patch area. In combination, this species shows contrasting characteristics of being a good initial colonizer requiring only relatively small habitat patches, but thereafter being highly vulnerable to stochastic extinction events due to environmental factors. This species probably uses only one food-plant on chalk grassland sites (*Viola hirta*), which can be present in large patches but is also highly vulnerable to stock grazing (high levels resulting in predation, low levels resulting in shading out) and desiccation of preferred large plants before larvae have fully developed (BUTT 1986). The large dark green fritillary population present on Porton Down is due to the fact that the primary grazer here is the rabbit, which avoids *Viola hirta.* The GLIM analyses showed a clear dependence on distance from Porton Down and other patches. The GLIM and IFM analyses shows a dependence on the few large colonies in the patch network to constantly re-colonize smaller sites, despite the dark green fritillary's high mobility and ability to 'find' new sites.

Small heath has mid-range values for most parameters except the one for colonization ability which is exceptionally high. This translates to the species having a poor ability to

colonize, although how much isolation is a factor is not clear as the parameter for the effect of distance on dispersal is of mid-range value. The relatively low value for critical minimum patch area may have something to do with this species' liking for edge habitat which increases with small patches (see Section 7.5). Although widespread geographically and over several habitats, this species has recently shown a severe national decline (Greatorex-Davies and Roy 2000), and it could be that a combination of habitat quality (see Section 4.26) and fragmentation has reached a critical point where its poor colonization ability is preventing recovery.

8.4.2 Linking IFM and Independent Analyses

The strong relationship between A_0 and 'inherent' butterfly population variability shown in Figure 8.1 is a clear indication of different sensitivities to factors such as environmental and resource changes by different species. Mechanisms relating to this relationship are clearly set out by the inclusion of patch area as a factor in population extinction probability in metapopulation dynamics (Hanski 1999). However, the exact nature of these mechanisms are not known, although one suggestion is the 'changing environment scenario'. This relates species' population ceilings, or carrying capacities (k in population dynamics), positively to patch size, but is complicated by independent factors acting on statistical variance around population growth. Larger patches are likely to be more heterogeneous than small ones and therefore when environmental stochasticity increases, essential resources are more likely to remain in the larger patches (Ehrlich and Murphy 1987). This is better referred to as the vegetation mosaic hypothesis (Short and Turner 1994). Clearly, the quantification of 'resource' in terms of species' habitat requirements, is

not a simple assessment of number of larval food-plants for example, as the order of species shown in Figure 8.1 would otherwise be very different.

The relationships between parameter estimates for effective strength of environmental stochasticity (x) and CANOCO axes from Fragmented Site ordinations show a great deal of consistency across axes and analyses (Figures 8.2 – 8.4). Species showing high values for x, and therefore low susceptibility to environmental stochasticity, are those which lie at the ends of the ordination axes related to landscape scale factors such as increased distance from potential source sites. Species showing low values for x, and therefore high susceptibility to environmental stochasticity, are those which lie at the ends of the ordination axes related to local scale factors (mainly habitat features). The implication here is that those species with low susceptibility occupy a more 'risky' ecological niche, as illustrated by positions on the ordinations. Species showing high susceptibility, however, do not risk involvement at the landscape level and probably occupy niches in areas of least heterogeneity. Inspection of the Figures shows one species in particular demonstrating a consistent position on this relationship, dark green fritillary. This species was shown to be very strongly (negatively) related to distance from Porton Down and inter-site distances in Chapters 6 and 7, but strongly related to its food-plant and preferred habitat (NVC type) in Chapters 4 and 5. Such clear and strong relationships at the two, local and landscape, scales, are unique among the study species and warrant further investigation.

Finally, the relationship between parameter estimates for the colonization ability of species, y, and the CANOCO axis from the Fragmented Site ordination (Figure 8.5), relates weakly to species' relationships with parameters for susceptibility to environmental stochasticity (Spearman Rank Correlation Coefficient, $r_s = 0.764$; $n = 7$, $0.1 > P > 0.05$). In

metapopulation dynamics terms, successful colonization of an empty habitat patch is probably most strongly related to propagule (i.e. colonization population) size (Ludwig 1996). This is in turn related to biological factors such as mode of reproduction and fecundity. However, niche width is also important, as generalists are regarded as better (or more commonly observed), colonizers than specialists (Ehrlich 1986). Looking at the species at the two ends of the graph in Figure 8.5, dark green fritillary and small heath, the niche hypothesis does not hold well as both species appear to require fairly specific habitat types, with dark green fritillary in particular, occupying a very narrow niche in terms of food-plant and preferred habitat (see Section 4.18). However, it may be that across the network of sites in this study, preferred resources are unusually abundant and niche width is less of a factor here. For dark green fritillary in particular, the IFM parameterisation (see Section 8.4.1) was useful in demonstrating a probable tendency to both colonize and rapidly become extinct. It may be that many of the species are still showing behavioural patterns which relate to past high landscape connectivity and habitat quality and which now conform to a consistent 'sink' metapopulation pattern (see Section 1.6).

9. DISCUSSION

9.1 INTRODUCTION

This discussion chapter will examine similarities and differences between the scales and methods of analysis in the previous results chapters. An overview of these conclusions will then incorporate theoretical and observational data from similar studies to attempt to form a synthesis.

9.2 LOCAL SCALE ANALYSES

Of the eighteen butterfly species analyzed by regression analysis, sixteen showed a significant model between presence/absence on transects and habitat and local scale environmental variables and only one, small blue, did not. Models could not be tested predictively between years for one due to low numbers. Ten of the sixteen species showed that models constructed from one year could successfully be used to predict presence/absence or population levels in subsequent (or previous years) with statistical significance. A further three species showed a measure of success with the between-year predictive power of the models but at $P > 0.05$. Only three species, grizzled skipper, small copper and hedge brown showed no apparent between-year predictive power of the models. Perhaps surprisingly, only eight of the seventeen species showing significant models in the regression analyses had larval food-plant as one of the explanatory variables. Only two species, chalkhill blue and hedge brown, had larval food-plant as the only explanatory variable in the model.

Butterfly distributions are dependent on a combination of environmental parameters including tolerance of climate, microclimatic development needs and distribution of adult nectar sources and larval food-plants (Dennis 1992). Of these, the closest relationship any butterfly has is its physiological one with its larval food-plants. Indeed, isolation of races within a species' geographical range is often accompanied by the evolution of different relationships with larval food-plants which are more suited to 'local' climate and habitats (Dempster 1995). In turn, the distribution of plant species is dependent largely on interactions between climate and soils which produce conditions of common physiological ecology for many other species and these therefore form characteristic communities (Rodwell 1991-2000).

It is not surprising therefore, that many of the species' models included explanatory variables that combined to give a broader picture of the overall resource requirements. For many of the butterfly species which apparently showed no selection on the presence of larval food-plant, the vegetation community provides a surrogate measure. For example, green hairstreak showed a preference for the CG2 NVC community; this community shows the highest frequency for two of the larval food-plants, common rock-rose *Helianthemum nummularium* and bird's-foot trefoil *Lotus corniculatus* (Rodwell 1992). Similarly, small heath showed a preference for three NVC communities, CG2, CG3 and CG6. These communities have the highest frequency values for two of this butterfly's most important larval food-plants, sheep's fescue *Festuca ovina* and red fescue *Festuca rubra* (Rodwell 1992). These associations are reinforced by both larval food-plant and its NVC community of highest frequency being selected together in the analyses (eg *Viola hirta* and CG3 for dark green fritillary, *Fragaria vesca* and CG7 for grizzled skipper).

The few exceptions to this rule were three species with grasses as larval food-plants. These species, small skipper, Essex skipper and ringlet, appeared to display a more diffuse type of habitat selection with the skippers being associated with lack of rabbit grazing and the ringlet selecting this plus cooler aspects and scrub with nectar sources. All of these observations agree well with the (relatively little) known requirements of the species (BUTT 1986).

9.3 LANDSCAPE SCALE ANALYSES

9.3.1 Fragmented Sites

Of the sixteen species for which there were sufficient data to perform regression analysis, twelve had local scale variables which were common to the Porton Down local scale models (including area of NVC types instead of presence/absence). Five species showed a relationship with patch area and only one, dark green fritillary, showed a relationship with distance effects.

9.3.2 Porton Down Patch Analysis

Of the seventeen species which had sufficient data to perform regression analysis, four produced models which were not significant at the $P < 0.05$ level while a further six had local scale variables which were common to the Porton Down local scale models. Six of the thirteen species with significant models showed a relationship with landscape scale variables (one with patch area, four with the nearest population node and one with average distance to population nodes).

The degree of similarity between selected variables showing 'landscape effects' in the Porton Down Patch analysis and those showing landscape effects in the Fragmented Sites analysis are summarized in Table 9.1.

Most obvious from these results is the lack of consistency of species showing sensitivity to landscape effects across the two analyses. Assuming this is not a simple result of anomolous methodology or an artefact of the data or statistics used, then there must be an explanation through different ecological and behavioural responses.

For those species with a relationship with Distance to the Nearest Population Node, there appears to be no association with the degree of coloniality as given in Warren (1992). Neither does there seem to be a relationship with mobility as given in Pollard and Yates (1993).

There does seem to be some pattern with the species showing a relationship with distance-related landscape scale variables in this analysis and those which had GLIM models with either poor between-year predictive power or which included a relatively large number of variables, or, in the case of small blue, did not produce a significant model in the Porton Down local scale analysis (Section 4.12).

Table 9.1: The degree of similarity between selected variables showing 'landscape effects' in the Porton Down Patch analysis and those showing landscape effects in the Fragmented Sites analysis. Species in bold show agreement.

Species	Landscape Effect? Porton Down Patches	Fragmented Sites
Small Skipper	No	**Yes**
Essex Skipper	**(No)**	**No**
Silver-spotted Skipper	No	?
Large Skipper	(No)	**Yes**
Dingy Skipper	No	**Yes**
Grizzled Skipper	Yes	**No**
Green Hairstreak	No	**Yes**
Small Copper	?	**No**
Small Blue	Yes	?
Brown Argus	**No**	**No**
Common Blue	(Yes)	**No**

Table 9.1 (Continued)

Chalkhill Blue	Yes	No
Dark Green Fritillary	No	Yes
Marbled White	**No**	**No**
Hedge Brown	Yes	No
Meadow Brown	Yes	No
Ringlet	?	No
Small Heath	***Yes(-ve)***	***Yes(+ve)***

(Yes/No) denotes models which approached significance i.e. P ≅ but > 0.05)

The implication here is that the best predictor of butterfly numbers or presence in these species is simply the distance from the core of the preferred habitat, which itself is poorly defined. In this case, the distance variables used (distance to nearest population node and average distance to nodes), are not really simple indicators of movement (as is the 'dispersal kernel' (Hanski 1999)), but is some function of a combination of local dispersal and local habitat availability. The reason for the poor between-year predictive power of these species' models is that their presence on sample transects away from their population nodes is less due to the presence of suitable habitat and more due to local dispersal during years of high population levels. It is not possible to say where this behaviour lies on the

scale of the relationship between local population dynamics and landscape scale (or metapopulation) dynamics.

One species, small heath, showed a relationship with patch area at both scales of GLIM analyses, but negative with the Porton Down Patches and positive with the Fragmented Sites. This species is known to be sedentary, often has two to three indistinct generations per year and appears to require early seral stage microhabitats within larger areas of diverse grassland (BUTT 1986; Shreeve 1995). Otherwise, it is widely recognized that this is one of the least known species in Britain (Oates 1995).

Usually, species which occupy early seral stage habitats are highly mobile due to the continual need for finding these temporary habitats (Oates 1995). However, the small heath is an example of an early seral stage occupant which also exhibits a strong sedentary nature and can exist in small 'closed' populations (Warren 1992). This behaviour is combined with the apparent need for edge microhabitats such as track edges or areas of grassland where sward height changes (BUTT 1986). There is therefore a clear correlation with patch area as these microhabitats are relatively scarce and therefore the probability of occurrence on a patch increases mainly as a function of total patch size. The different relationships shown in the two analyses above are almost certainly due to the type of data ie transect counts at Porton Down (producing population density estimates) and presence/absence on the Fragmented Sites (producing probabilities of occurrence). A negative density-area relationship was found for the Glanville fritillary *Melitaea cinxia* by Hanski *et al* (1994). Although no explanation for this relationship was found (there was no correlation with isolation), this species occupies habitat of a very patchy nature, perhaps providing a parallel with small heath in this study.

Generally, therefore, the same (or similar) ecological processes may well be acting within the two study systems but with different apparent outcomes. Processes such as environmental stochasticity would clearly be more likely to produce extinctions among the Fragmented Sites while exactly the same perturbations would produce more subtle changes in population density gradients among the Porton Down Patches.

9.4 COMMUNITY ANALYSIS

9.4.1 Local Scale Data

The analyses of both Porton Down and Fragmented Patch local scale data proved very useful in both emphasising the results of the GLIM analyses and demonstrating the species' affinities in terms of habitat and (micro-)site selection. For the rarer species, such as wall and adonis blue, positions on the CANOCO ordination plots accurately reflected their known requirements. Some 'extremes' of habitat selection were also shown, such as that of the two 'small' skippers, Essex and small skipper, at one end of the ordination and adonis blue and silver-spotted skipper at the other. Equally striking was the degree of neutrality of meadow brown, which is interesting for a species which can show a high degree of polymorphism (Brakefield 1990; Ford 1975; Brakefield and Shreeve 1992).

One additionally useful aspect of these analyses was the contrast between the 1995 and 1997 Porton Down local scale data. These showed how between-year climatic differences, combined with population changes (over 90 per cent reduction in large skipper numbers occurred between these years), can produce quite different profiles of habitat selection. Some of these species show regular population fluctuations due to external factors such as

changes in larval food-plant demography. Such a species is small blue (Morton 1985). Others may be on the edge of their natural range or may be near the limits of their ecological tolerance on the well-grazed grasslands at Porton Down. The large skipper would seem to be a good example of the latter.

Finally, the extent to which some species with 'closed' populations (Warren 1992) could be positively managed on a local scale with spectacular results was demonstrated by the comparison between Porton Down and Fragmented Patch local scale data. The two lycaenids, adonis and chalkhill blue, showed huge population densities on some relatively small, but prescriptively managed (by stock grazing) sites. How much immigration of individuals from other sites is required to maintain these levels is unknown.

9.4.2 Landscape Scale Data

9.4.2.1 Porton Down Patches

Community analysis of Porton Down Patch data largely substantiated the GLIM analyses in that the 'landscape scale' variables of distance to population nodes did not appear to relate truly to real landscape scale factors, while patch area was relatively unimportant compared to local scale variables such as major contrasting NVC types, sward structure and grazing pressure. It must be accepted that the difficulties of 'imposing' landscape scale factors on a single, large area of habitat with indistinct patch boundaries and unmeasured rates of migration between patches has limitations for interpreting the possible processes involved. However, a few species, such as Essex skipper and small copper, which have generally not been highlighted by the other analyses, showed some

sensitivity to this approach and more detailed studies involving measurement of processes mentioned above may reveal some interesting results.

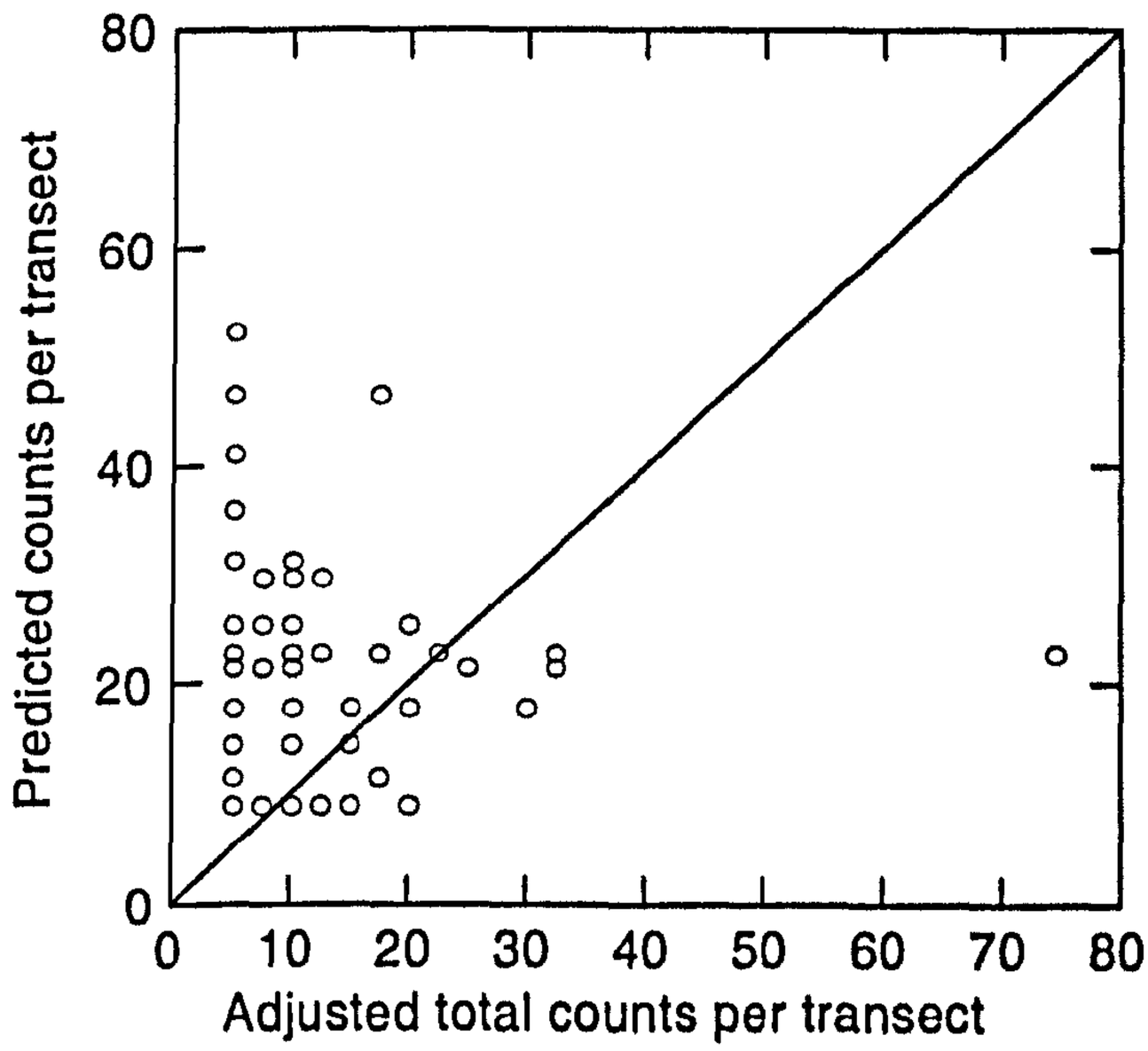
9.4.2.2 Fragmented Sites

These analyses fairly successfully teased out the relative importance of patch area and isolation (which have been termed the first-order landscape effects on population biology (Hanski 1999) see Section 1.2.3) in comparison with local scale habitat and environment. Patch area appeared to have the strongest effect on species' presence/absence for several species, particularly those with requirements for short turf such as silver-spotted skipper, wall and adonis blue. Clearly, the increasing probability of 'rare' micro-habitats occurring on larger patches is the driver here. Interestingly, the relationship with patch area shown by small heath in the GLIM analyses was continued here, with this species' need for a diversity of edge-type micro-habitats ultimately being reflected by a positive relationship with patch area.

The most anomalous species in these analyses, however, was the dark green fritillary. This species appeared to show a complete dependence on a combination of distance from its major 'source' site Porton Down and the average distance between all sites in determining its presence at a site in the patch network. The degree of dependence can be demonstrated by Figure 9.1 which shows the predicted populations on Fragmented Site transects (from the Porton Down local scale 'habitat' model) plotted against observed transect count totals adjusted by the regression Adjusted Index = 5.238+2.476*Total Transect Count (shown in Figure 2.4b). The bold line shows where points would lie if the relationship was 1:1. The vast majority of data points lie above this line however. It is clear that habitat quality alone

severely underestimates the numbers seen on the majority of samples within patches and that other factors - migration from source populations - is of over-riding importance for all but the smallest populations.

Figure 9.1: The relationship between predicted populations on Fragmented Site transects (from the Porton Down local scale 'habitat' model) against adjusted observed transect count totals



9.5 INCIDENCE FUNCTION MODELS (IFMs)

IFMs were run for seven species which were present in the patch network within the criteria set by Hanski (1994). Standard errors over ten model runs were acceptable for all modelled parameters and for all species and one can use these results with some confidence assuming some data constraints and the IFM algorithmic constraints (Moilanen

2000). Parameter estimations generally fitted extremely well with current knowledge of species' biology and population ecology. One extraordinary finding, which fitted well with the GLIM and CANOCO analyses but is not backed up by current knowledge, was that for dark green fritillary. This species showed an almost complete dependence on the few high quality 'source' sites from where it appears that many individuals temporarily colonize other patches. The reason for its high susceptibility to environmental stochasticity is not known but may be linked to the ecology of its larval food-plant *Viola hirta*. *Viola hirta* is a plant which is highly sensitive to grassland management despite being a moderate stress-tolerator (Grime *et al* 1988), and is likely to fluctuate in abundance from year to year, particularly where stock grazing is used.

At the other end of the scale, small heath showed very poor colonization ability which is linked to the species' apparent need for edge microhabitats. This is in turn linked to patch area (which was substantiated by the low value for critical minimum patch area), and diversity of grassland communities. Such an ecological profile does not augur well for the species in an increasingly fragmented and poorly managed set of patch networks. Indeed, a continual and significant decline in monitored populations of small heath has occurred over the past 15 years (Greatorex-Davies and Roy 2000).

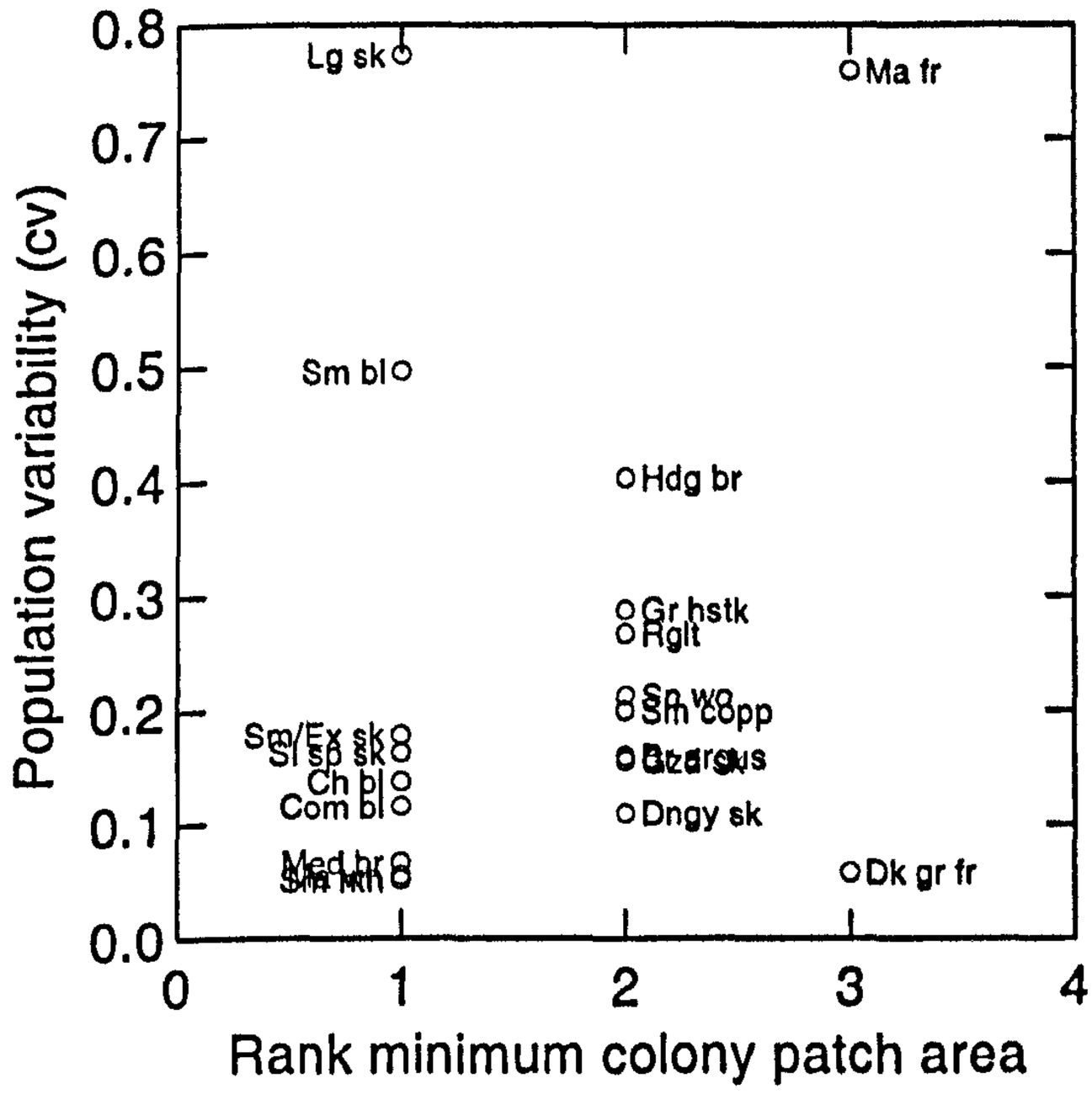
Perhaps surprisingly, the species which showed least susceptibility to environmental stochasticity included the two chalk grassland skippers, grizzled and dingy skippers. The grizzled skipper is a naturally uncommon species, occurring at low densities even on prime sites (Brereton *et al* 1998). It is perhaps less surprising in this light, that the species shows resilience to environmental stochasticity and therefore general resistance to local extinction. The dingy skipper showed less resilience to environmental stochasticity and

occurs at only slightly higher densities than the grizzled skipper at most sites. This species has shown a significant decline on monitored sites in the last 15 years (Greatorex-Davies and Roy 2000) and it may be that critical levels have been reached in terms of landscape connectivity and management.

The relationship between population variation and critical minimum patch area for the few species modelled with the IFM can be extended by using Warren's (1992) groupings of 'closed population' species under minimum areas from which colonies have been recorded. Using these groupings as ranks, a plot of minimum area against (log) population coefficient of variation (CV) on Porton Down's grassland BMS transect shows a positive relationship with three outliers (Figure 9.2). The correlation is therefore low (Spearman Rank Correlation Coefficient $r_s = 0.239$; n = 18, NS). Grizzled skipper was added ranked 2 (from IFM estimates of A_0) as this species did not appear in the original Table. If data from Porton Down's woodland ride BMS-type transect are substituted for large skipper and ringlet (as populations here are much less marginal compared to the well-grazed grassland ones) and data for marsh fritillary on this transect are also added, the relationship is greatly improved.

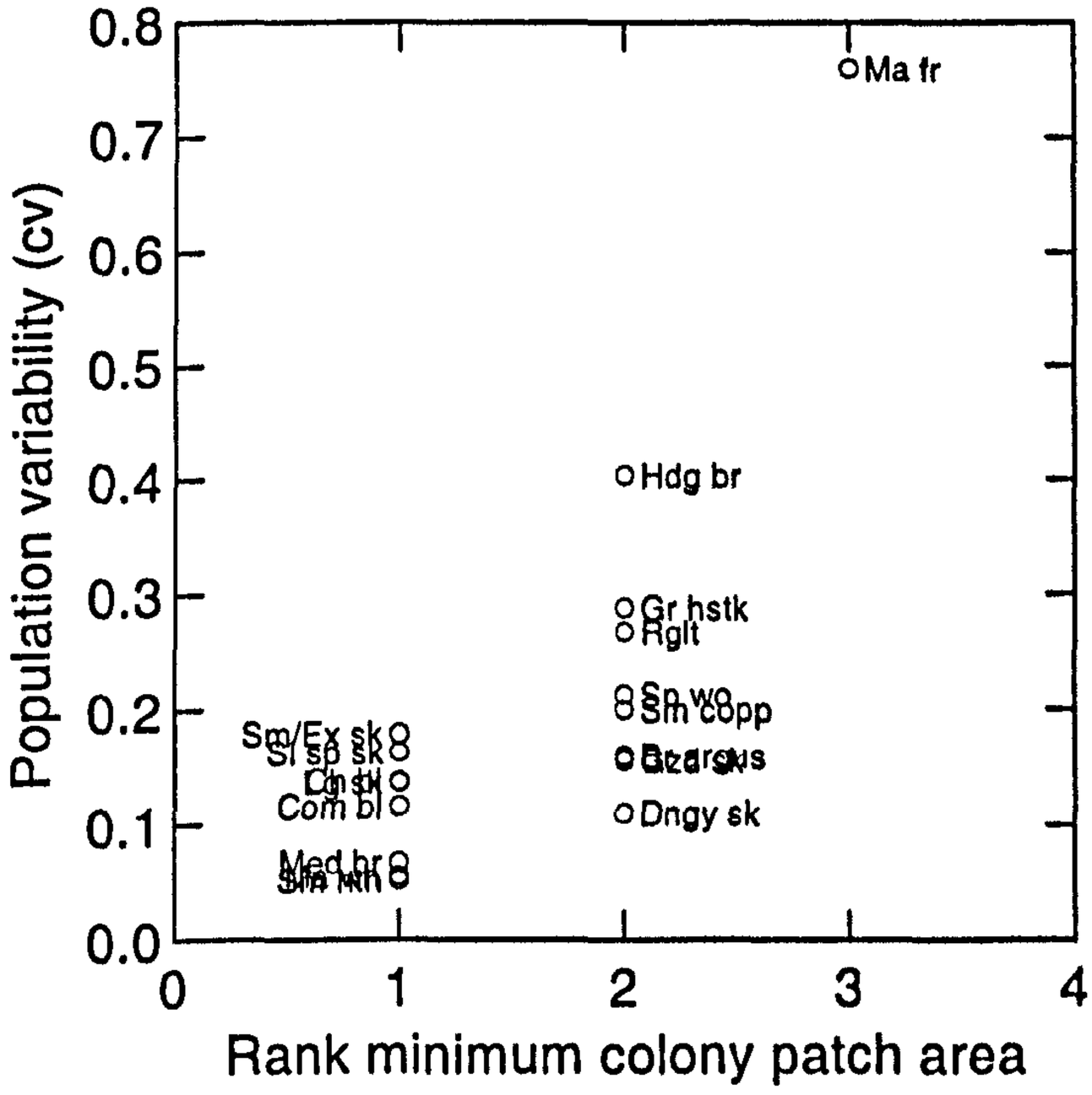
Two anomalous species in this relationship are small blue and dark green fritillary. As previously discussed (Section 4.12), small blue appears to show highly volatile population fluctuations which track its only food-plant, *Anthyllis vulneraria*. For this reason, this species has an unusually large population CV and has presumably adapted genetically and behaviourally to regular local effective extinctions.

Figure 9.2: The relationship between rank minimum colony area and (log) population coefficient of variation (CV) on Porton Down



Dark green fritillary, on the other hand, appears to show unusually small population fluctuations at Porton Down. An analysis of CVs at other sites locally show figures of around 0.3 to 0.5 to be more typical (Taverner 1999; Fuller 1999). Treating these two species as outliers (Jongman *et al* 1987), their removal greatly improves the overall relationship (Figure 9.3) which is highly significant (Spearman Rank Correlation Coefficient $r_s = 0.718$; $n = 16$, $P < 0.005$).

Figure 9.3: The relationship between rank minimum colony area and (log) population coefficient of variation (CV) on Porton Down (two outliers removed)



For the vast majority of species in this study therefore, the relationship between population variation (as measured by population CV), and measures of minimum patch/habitat areas appears to be strong.

The final question in relation to patch area would be where it lies in importance between the true metapopulation view (patches are relatively separate habitat units, with populations acting in isolation apart from occasional inter-site migration), and the landscape context view (patches are connected by corridors of varying permeabilities producing a complex mosaic of patches and inter-patch habitats). In this study, the

selection of patch area as an important factor in regression models was restricted to species known to be relatively sedentary (see Section 6.26) and show a 'closed' population structure (Warren 1992). In addition, community analysis showed patch area to be strongly related to within-patch quality variables (Chapter 7), with inter-patch distance occupying a different vector. The conclusion for this set of study sites must be therefore, that patch area relates strongly to within-patch local scale habitat quality which then becomes a strong determinant of landscape scale metapopulation dynamics as inferred in the vegetation mosaic hypothesis (Short and Turner 1994 and see Section 8.4.2). For most species, the large rescue effect of the Porton Down site and the few other moderately large sites with high quality habitat, plus the connectivity of the landscape, has produced a system more akin to Weins' Landscape Ecology model (Section 1.7).

9.6 LINKING THE ELEMENTS: A SYNTHESIS

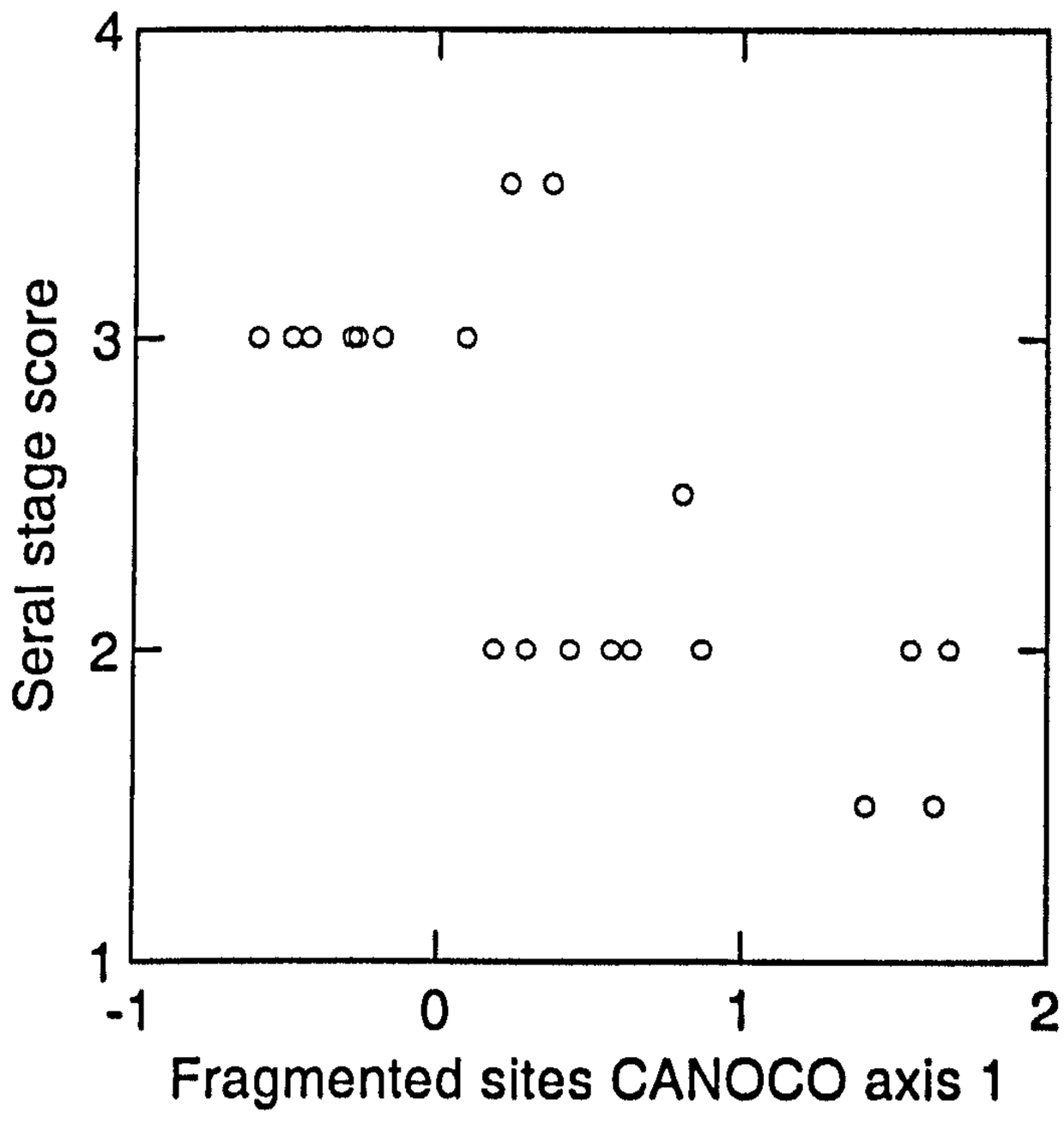
When IFM and CANOCO analyses were compared (Chapter 8), there were several statistically significant correlations between IFM parameters for the degree of susceptibility to environmental stochasticity (x) and the colonization ability of a species (y) and species' scores on the ordination axes. For x, this relationship was even stronger when only the landscape variables distance from Porton Down (the major 'source' patch), average distance between patches and patch area were used to generate species-environment ordination axes. Clearly, the more isolated a species becomes in ecological terms, the more resilient it needs to be in order to resist widescale extinction among patch networks.

For colonization ability (*y*), the relationship appears to be strongly oriented towards issues of habitat quality and structure, which in turn is related to patch size due to the rarity of 'quality' habitat in small patches. The question is how does this habitat quality issue relate to metapopulation ecology?

Species' positions along the Fragmented Sites CANOCO axis 1 (Figure 7.7) possibly reflect the way their population ecology determines how they move about the landscape and how they use the available habitat when they settle. In order to test this theory, species scores on axis 1 were regressed against a number of independent measures of habitat selection and occupancy. Figure 9.4 shows the relationship between species' scores and seral stage scores as given in Dennis (1992). Younger seral (successional) stages score lower. Where a range of scores was given, a median value was taken. This relationship is highly significant (Spearman Rank Correlation Coefficient $r_s = -0.723$; $n = 20$, $P < 0.001$).

Species towards the positive end of axis 1 require well-grazed, more two dimensional but often relatively species-rich habitats (not 'species-saturated' as in higher seral stages). These habitats are likely to be variable in quality over time and such species need to have some inherent resistance to extinction, which has been shown to be the case above in terms of lower susceptibility to environmental stochasticity.

Figure 9.4: The relationship between species' scores on Fragmented Sites CANOCO axis 1 and seral stage scores



Saccheri (1998) showed that the average number of heterozygous loci in 42 populations of Glanville fritillary was much lower in those populations at greater risk of extinction due to ecological factors. This was usually due to a high level of inter-sibling mating. Although this may be an extreme example, it nevertheless demonstrates the pressures on such species to evolve genetic robustness. The additional price paid for this combination of attributes is relatively poor powers of dispersal. However, individuals can still make long migrations to find suitable habitats to colonize as has been shown by mark-recapture studies on silver-spotted skippers whose longest observed colonization distance was nearly 30 times further than the longest observed migration distance (Thomas and Jones 1993).

Recent work has also shown that more isolated populations of this species have rapidly evolved individuals adapted for longer migration flights (Hill *et al* 1999).

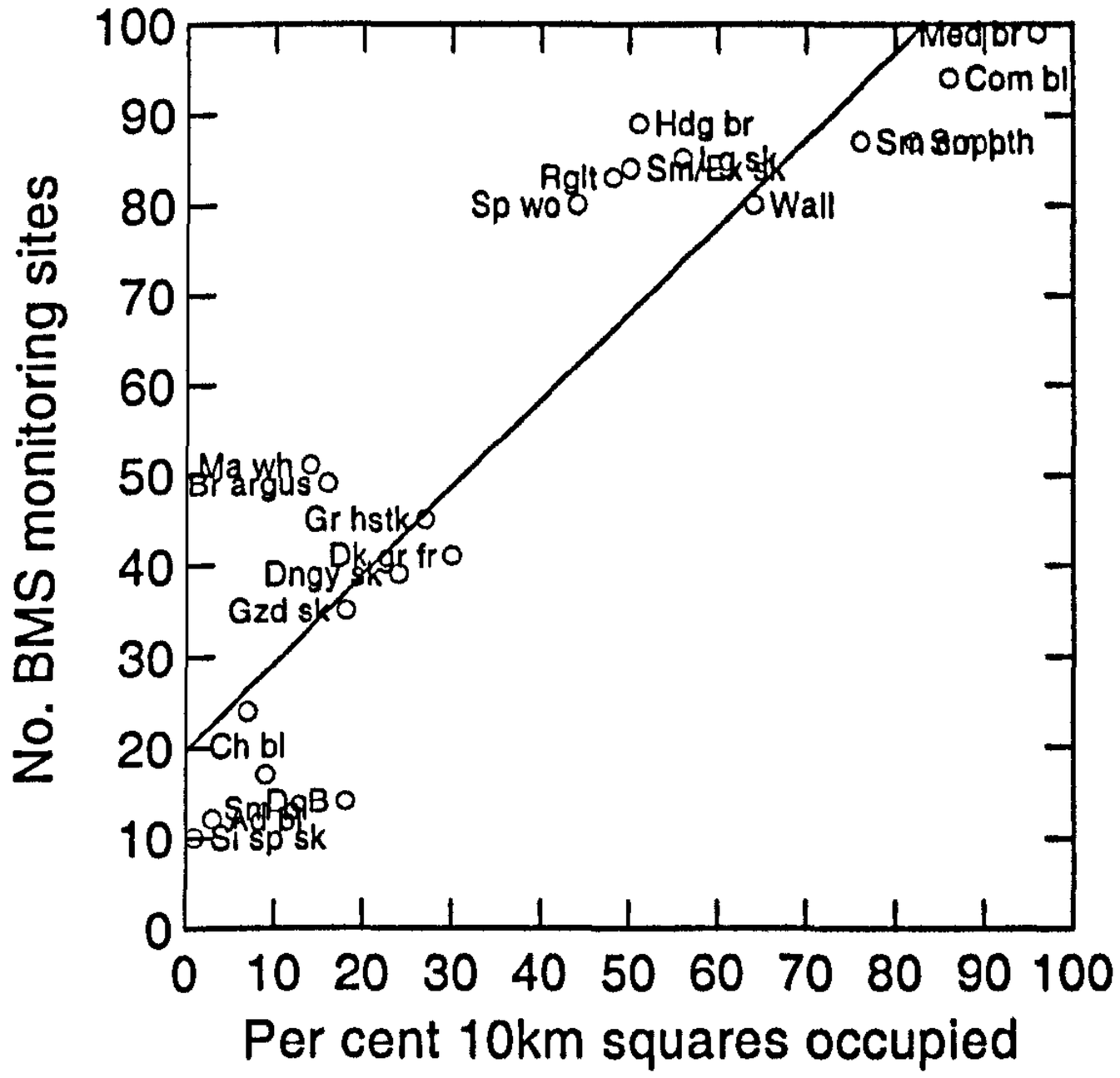
Species in the mid-range of axis 1 tend to have moderate to good powers of dispersal, as measured by the effect of distance on dispersal (α) in the IFM. Some evidence is shown by three mark-release-recapture studies in Hanski and Kuusaari (1995) who quote longest observed migration distances of 7.3 km for marbled white and 0.3 km for both silver-spotted skipper and adonis blue and a more recent study by Baguette *et al* (2000) where the longest distance moved by marbled white was 2.5 km but only 0.75 km for small blue in the same patch network. Species in the mid-range group of axis 1 tend to be those which show medium specialization both in terms of the number of larval food-plants (Spearman Rank Correlation Coefficient $r_s = -0.414$; $n = 20$, $0.1 > P > 0.05$ between axis 1 score and number of principal larval food-plants) and in terms of local habitat and microhabitat requirements as demonstrated by the relationship with seral stages shown above. However, both larval food-plants and preferred habitat would be relatively rare in the general landscape and these species would find intervening habitat relatively alien to them. The group does include species which have 'good' years when high population levels trigger dispersal into new areas. These occurrences may be regionally or even nationally synchronized, as with brown argus in 1996 and grizzled skipper in 1997 (Greatorex-Davies and Pollard 1997), or may be more local and unsynchronized as with chalkhill blue (Fuller 1995b).

Species at the negative end of axis 1 tend to be good dispersers, either due to being strong fliers who can migrate easily between suitable patches (as the dark green fritillary), or due to viewing the landscape as a series of highly suitable patches of habitat connected by less

suitable, but adequate habitat. Thus, this group consists largely of species which are larval grass-feeders, utilising several common species, and can use areas of ephemeral vegetation as breeding habitat. Recent work has shown a possible link between an increase in abundance of several of these species and that of some common plant species such as couch *Elytrigia repens* and nettle *Urtica dioica* (Smart *et al* 2000).

It is useful at this stage, to examine the relationship between species' general ecology in the landscape (from the previous analyses) and measures of regional distribution. Data are available from two sources, the BMS (Greatorex-Davies and Roy 2000) and the most recent Atlas of British Butterflies (Heath *et al* 1984). A plot of the number of BMS sites at which species were found against the percentage of occupied 10km squares in the atlas shows that nearly all species are 'over-represented' in the BMS as shown by the linear regression trend line (Figure 9.5), which would lie at 45 degrees and arising from the origin if the two distributions were equal. There is, however, a strong agreement between the two measures of regional distribution overall (Spearman Rank Correlation Coefficient $r_s = 0.903$; $n = 20$, $P < 0.001$). One problem with using the two methods is that the atlas data are now at least 18 years old and it is known that most of these species have changed in both range and abundance over the past decade (Cowley *et al* 1999; R. Fox, Butterfly Conservation, pers. comm.).

Figure 9.5: The relationship between the number of BMS sites at which species occur and the percentage of occupied 10km squares in the 1984 Atlas



Equally, the BMS sites tend to be nature reserves and other sites of high butterfly species richness with large populations (Pollard and Yates 1993). Species could lie above or below the trend line for two reasons: firstly, they may be exaggeratedly over- or under-represented at the BMS sites and secondly, populations have changed greatly relative to a reference period when it can be assumed they were all positioned closer to the line.

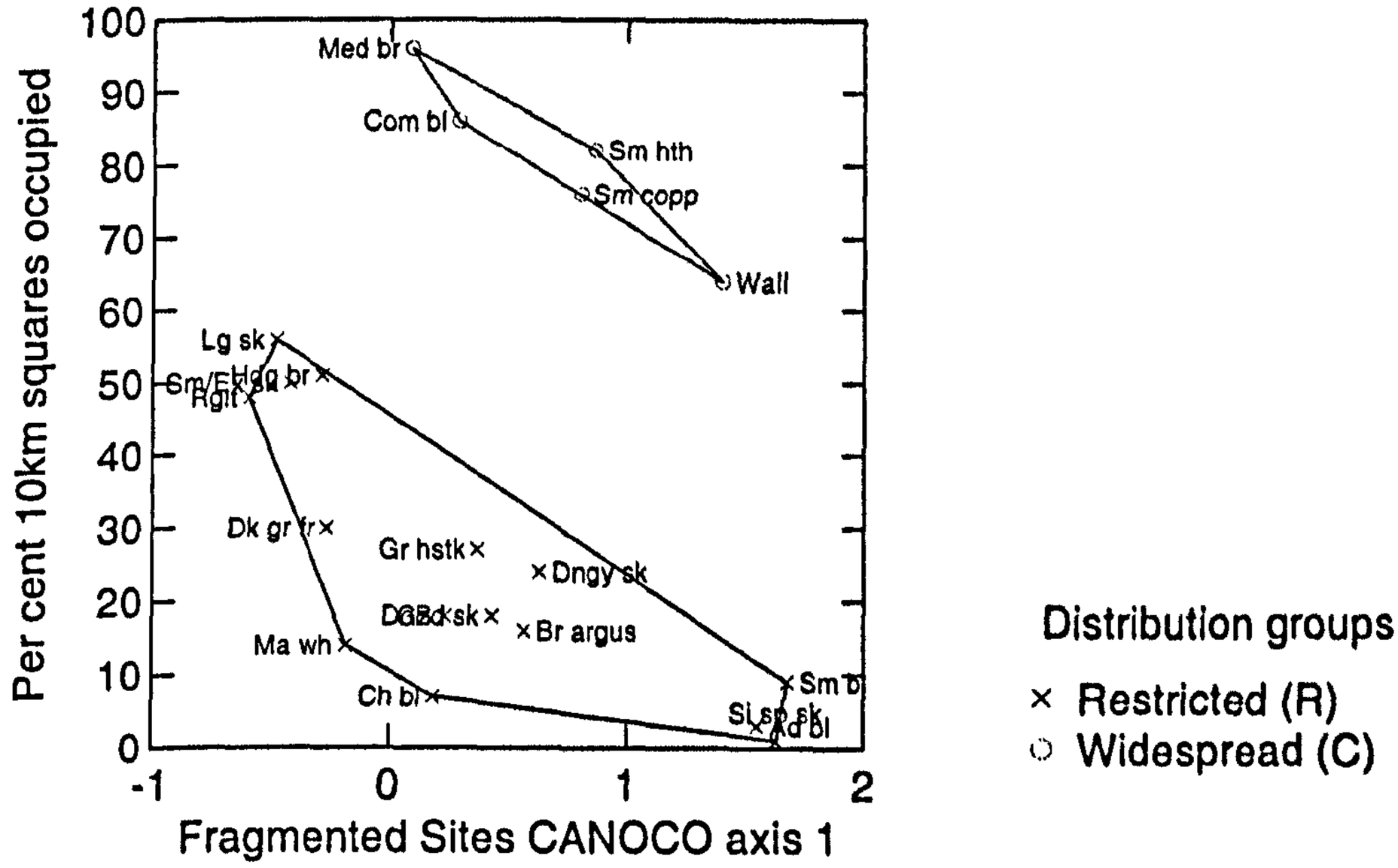
Figure 9.6a shows the relationship between CANOCO axis 1 scores for Fragmented Sites and percent of 10km squares occupied from the Atlas data. Given the scatter, it is not surprising that the relationship is not significant for all the species (Spearman Rank

Correlation Coefficient $r_s = -0.312$; $n = 20$, $0.2 > P > 0.1$). However, there appears to be two separate groups on the plot. The group towards the top right sector (the 'C' group) of the plot are widespread and (at the time of the Atlas work), relatively common species in Britain. The group towards the bottom left sector of the plot (the 'R' group) are those of a more restricted nature. Most distributions in this group are restricted by climate or geology or a combination of both. A few, particularly dark green fritillary, green hairstreak and small blue are restricted due to other, largely unknown factors, although grassland 'quality' is probably important (Warren 1992). Taken as distinct groups, the 'R' group shows a significant relationship with axis 1 scores (Spearman Rank Correlation Coefficient $r_s = -0.779$; $n = 15$, $P < 0.001$), but the 'C' group does not (Spearman Rank Correlation Coefficient $r_s = -0.9$; $n = 5$, $P = 0.1$). This latter group does show a strong trend, however, and probably suffers statistically from having only a few members. Linear regression trend lines are shown plotted for each group separately in Figure 9.6b and have remarkably similar slopes.

Further analysis of the relationship between overall and within-group axis 1 scores (Figures 9.6a & b) and some selected life history factors is very revealing and is summarized in Table 9.2.

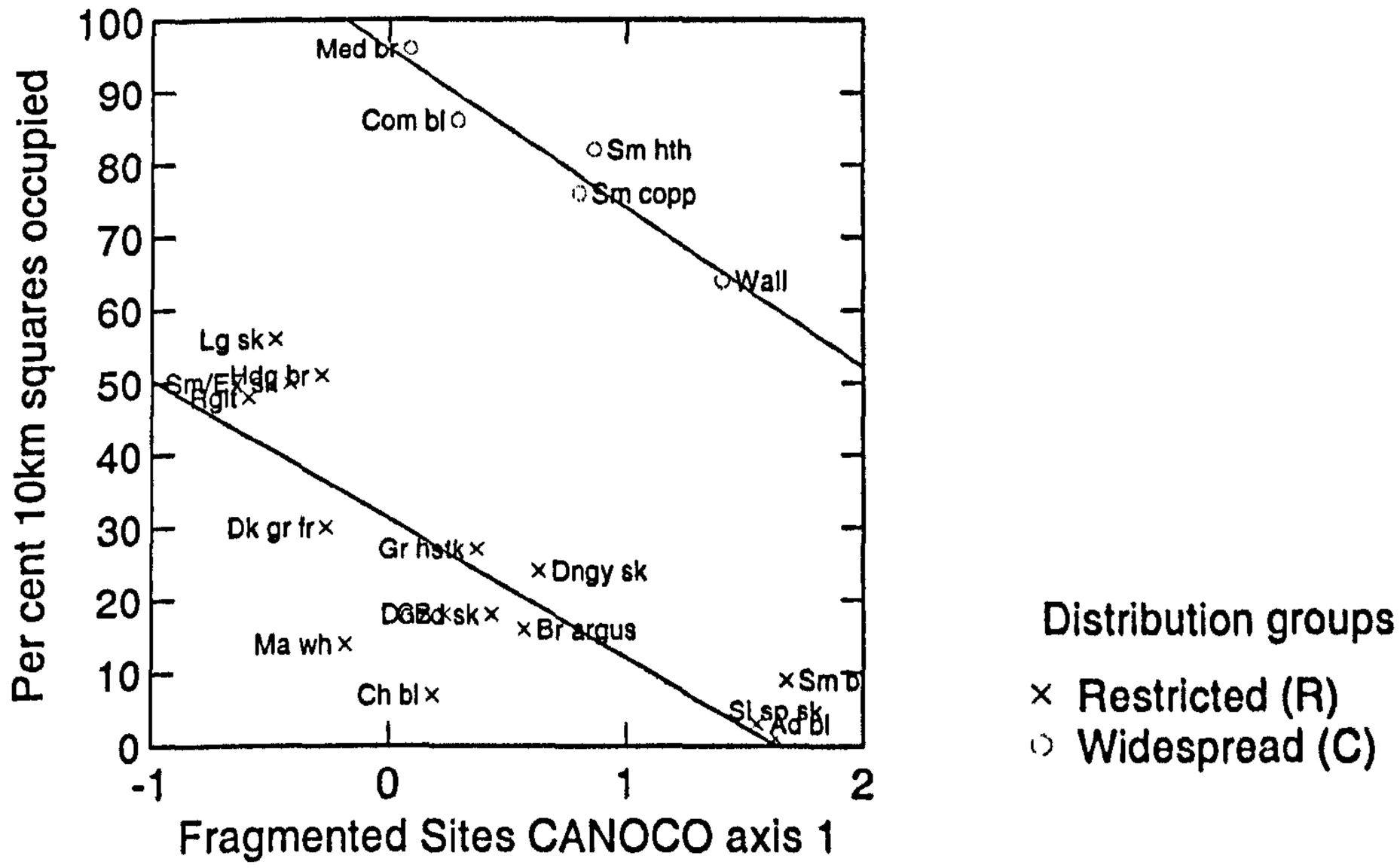
The number of main larval food-plants is taken from the same sources as for the GLIM analyses (BUTT 1986; Pollard and Yates 1993; Dennis 1992 and see Appendix 5) and number of generations from Pollard and Yates (1993).

Figure 9.6a: The relationship between CANOCO axis 1 scores for Fragmented Sites and percent of 10km squares occupied from the 1984 Atlas



There were also between group differences among these two life history factors, with the 'C' group showing a tendency towards using more food-plants (polyphagy) and the 'R' group towards few or single food-plants (mono- or oligophagy) (Mann-Whitney U statistic U = 60.0; df = 1, P = 0.044), and the 'C' group showing a tendency towards multivoltinism compared to the generally single brooded 'R' group (Mann-Whitney U statistic U = 62.0; df = 1, P = 0.011).

Figure 9.6b: The relationship between CANOCO axis 1 scores for Fragmented Sites and percent of 10km squares occupied from the 1984 Atlas (group regression lines shown)



There is a distinct 'cline' within the groups in relation to voltinism, with species at the top left end of each group in Figure 9.6 being single brooded. However, the 'C' group shows a trend from the meadow brown, which, although being single brooded, shows great flexibility in emergence date and length of its single generation (Brakefield 1987), through common blue which is univoltine in the north of Britain, bivoltine in the south, to small heath, small copper and wall which have up to three broods in the south of Britain (a partial third for wall).

Table 9.2: Summary of tests for correlations between CANOCO axis 1 scores and life history factors

	Spearman Rank Correlation Coefficient r_s		
a) No. Main Food-plants	All species	'C' group	'R' group
	-0.414 (*)	-0.154	-0.670 **
b) No. Generations	All species	'C' group	'R' group
	0.610 **	0.707	0.560 *

Asterisks indicate the statistical significance of correlations: * $P < 0.05$, ** $P < 0.01$, (*) approaching significance at $0.1 > P > 0.05$.

In many ways, the differences above reflect the species' abilities to cope with 'range' and its correlated components of climate and resource predictability. The more widespread a species, the more it needs a larger number of resource alternatives to survive environmental changes (Dennis 1993). It also needs flexibility in terms of reproduction, with species showing inflexible, short and seasonally fixed flight periods being much less likely to be found across wider latitudes. Dennis (1993), ranked species according to their 'internal' i.e. biological, vulnerability relating to their capacity to withstand changes and their flexibility to respond to changes. The two measures are a sum of factors related to latitudinal range in Britain, general distribution, food-plant utilisation, food-plant

abundance, vulnerability of seral stage occupied and range of semi-natural habitats occupied (capacity to withstand change), dispersal ability, voltinism, length of flight period and overwintering stage (flexibility to withstand change). The overall index (minus the distributional factors) correlates very strongly with the number of occupied 10km squares in the Atlas (Spearman Rank Correlation Coefficient $r_s = 0.799$; $n = 20$, $P < 0.001$), as do the separate indices for 'capacity' ($r_s = 0.767$; $n = 20$, $P < 0.001$), and 'flexibility' ($r_s = 0.707$; $n = 20$, $P < 0.001$). While, as Dennis points out, there are exceptions within the trends, this degree of correlation between range and vulnerability agrees well with current (at that time) population and range trends, especially within taxonomic groups.

The three measures, the two discussed above plus the CANOCO axis 1 scores, can be viewed as measures of the species' ecology within the landscape (CANOCO axis 1 score), their regional distribution (per cent 10km squares occupied in Britain) and their biological robustness (Dennis' vulnerability scores minus distribution). This relationship is shown in Figure 9.7. The major 'step' between the 'C' and 'R' groups is very evident on the biological robustness axis.

One way of investigating the processes behind this group difference is to plot CANOCO Fragmented Site axis 1 scores against the more recent, but less strict (see above), measure of regional distribution, the number of BMS sites at which species occur. This plot is shown in Figure 9.8. Several of the rarer species (the 'R' group in Figure 9.6a & b) show increases in their relative values between the two regional distribution measures, including dingy and grizzled skippers, brown argus and marbled white. These probably reflect the quality of the BMS sites, although it is known that brown argus and marbled white have

shown recent increases in their populations and distributions (Greatorex-Davies and Roy 2000). The biggest difference, however, is shown by the group of five larval grass-feeders which were at the top left end of the 'R' group in Figure 9.8. These species, small/Essex skipper (counted as one in the BMS), large skipper, hedge brown and ringlet, have all increased considerably in their relative abundance between the two measures. All five species are known to have increased in range and abundance, despite in some cases, having previously contracted in range around the time of the Atlas (Heath *et al* 1984). In addition, these were among a group of nine species, out of a total of seventeen studied, who showed a relatively large increase in food-plant cover between 1978 and 1990 in the study by Smart *et al* (2000).

Interestingly, meadow brown and wall were the other two species in the group that are included in this study to show both relatively large increases in food-plant cover and recent increases in abundance on the BMS distributions (Greatorex-Davies and Roy 2000).

Figure 9.9 shows how the apparent changes in regional distribution might be explained according to the landscape model of Weins (1997). The 'connectivity threshold' is the region on the graph where loss of habitat becomes critical according to where a species lies on the 'sensitivity' (y) axis. Loss of all semi-natural habitat has been progressive over the last 5 decades (Bunce *et al* 1999), and particularly on calcareous substrates (Keymer and Leach1990; Burnside *et al* 1998). Some species will have hit the critical threshold some time ago, and are now in a situation where true metapopulation processes are dictating population survival probabilities in a series of small habitat patches surrounded by an essentially alien landscape.

Figure 9.7: The relationship between species' ecology within the landscape, regional distribution and their biological robustness (see text for details)

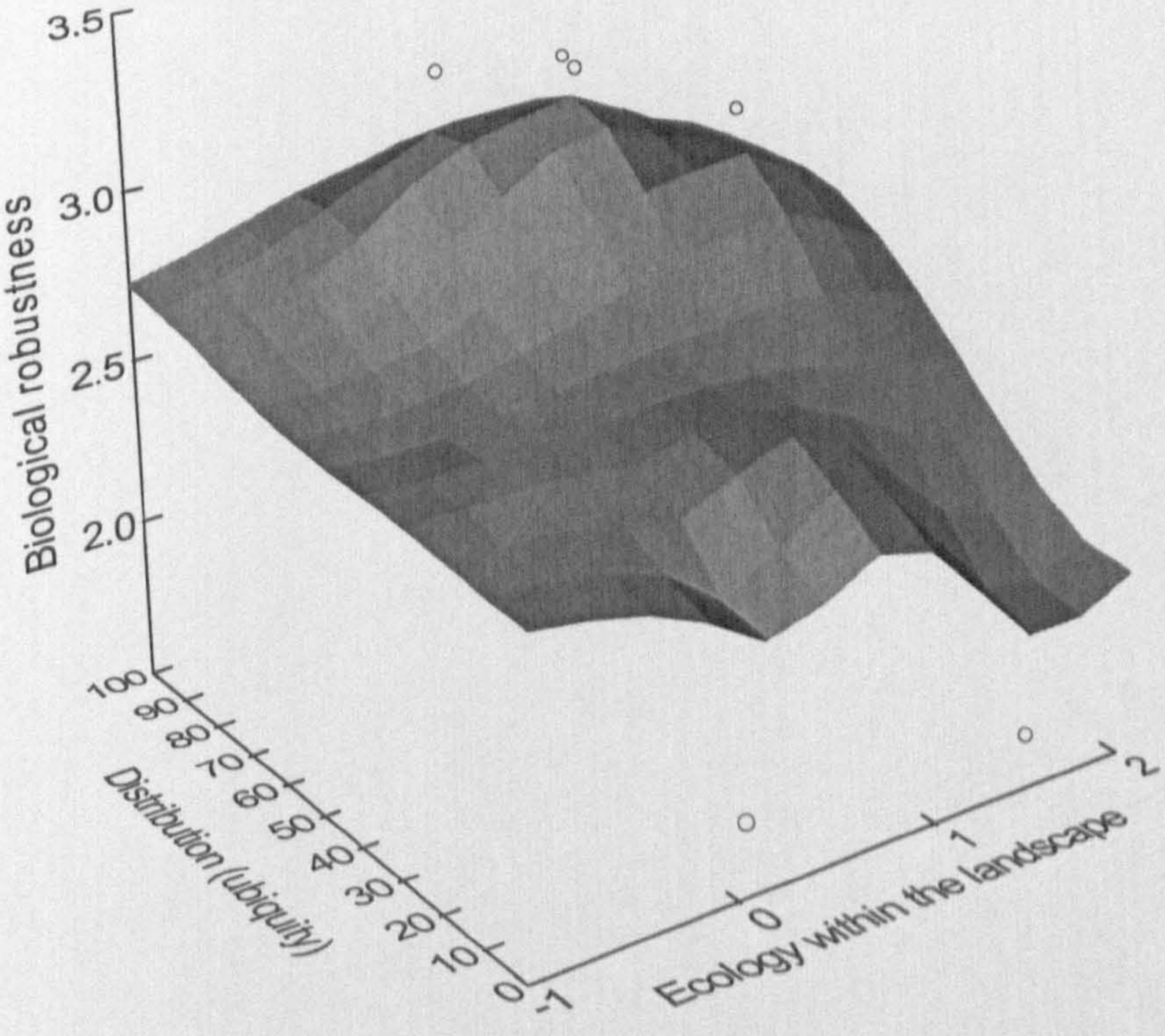
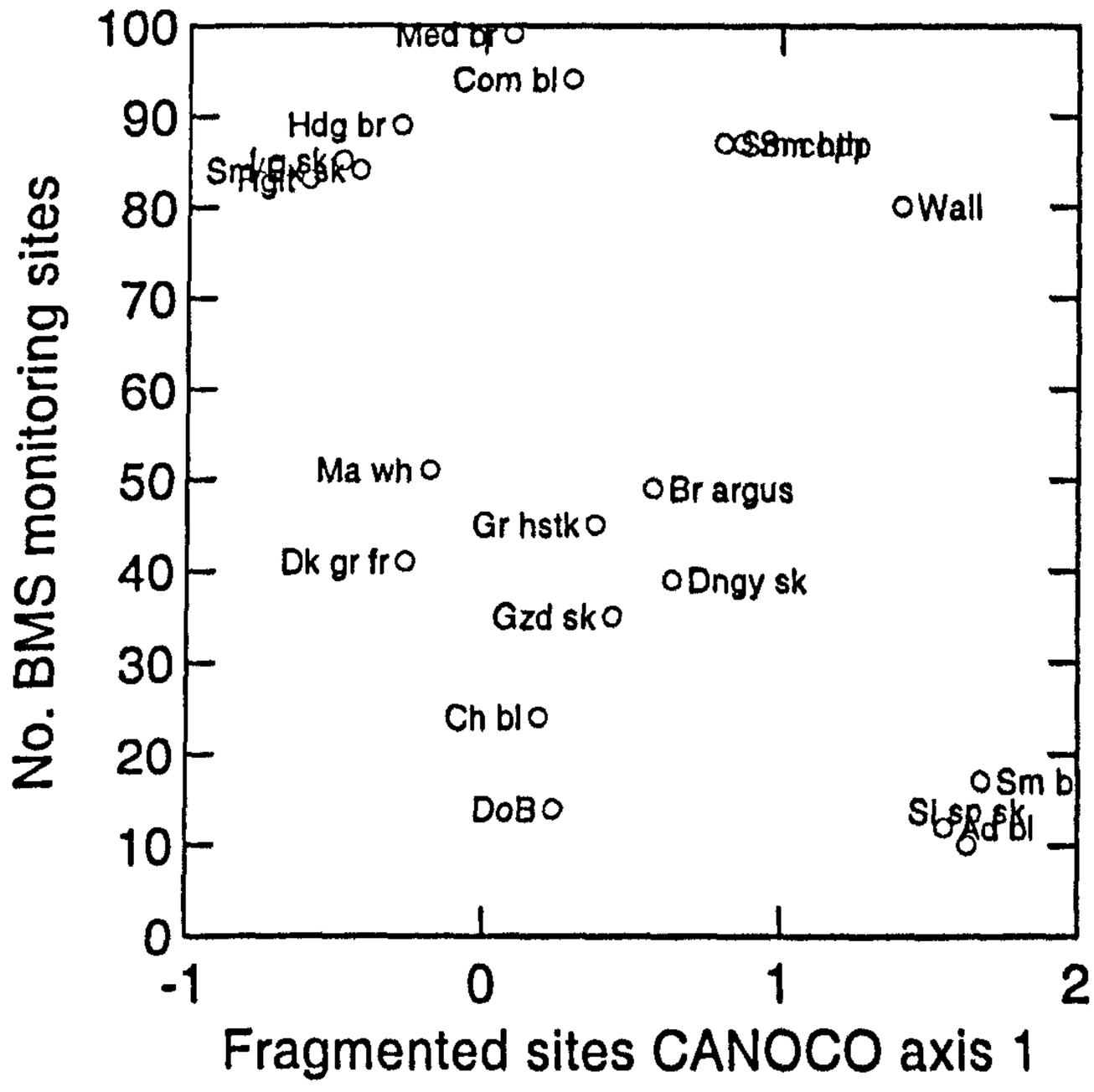


Figure 9.8: The relationship between CANOCO Fragmented Site axis 1 scores and the number of BMS sites at which species occur



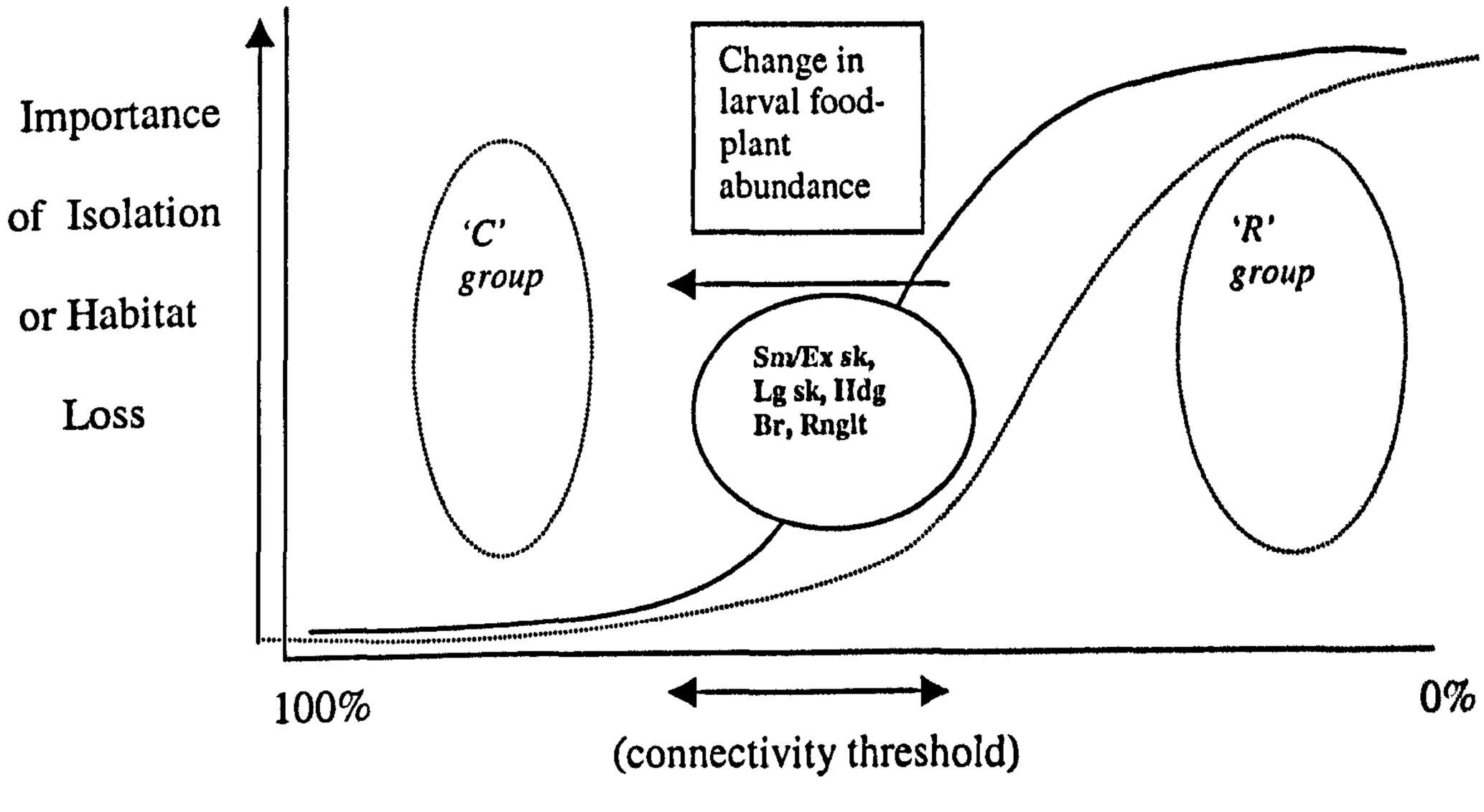
These are generally akin to the 'R' group shown towards the right hand end of Figure 9.9. Other species, particularly those which use the landscape as a series of highly suitable patches of habitat connected by less suitable, but adequate habitat (see above), are still above any critical threshold and are shown as the 'C' group to the left of Figure 9.9. The five species of particular interest here, are shown as a separate group, who had probably reached the area of critical threshold and were showing a decline as seen in the Atlas study, but have been 'pushed' back over the threshold, perhaps due to the increase in abundance of their larval food-plant as discussed above. It is important to point out that it is the threshold which has changed position rather than the species' which would tend to show relatively fixed

behaviour. Rather, these species' behaviour will have been in response to a change in resources.

The most recent data from Butterfly Conservation's Millenium Atlas work (Asher *et al* 2001) and kindly provided by Dr R. Fox (pers. comm.) does appear to corroborate this theory. Changes in per cent occupation of 10 km squares between 1970-1982 and 1995-1999 show between -5.7 and -14.5 for the 'C' group while the floating group show between -0.2 and +12.8. These two groups are therefore converging as in Figure 9.9. The 'R' group shows a great mixture of changes from positive to negative, with Duke of Burgundy showing the greatest decrease (-14.2) and marbled white and brown argus both showing an increase of +9.8.

Only a re-analysis of species' relationships with habitat and landscape factors would show whether the floating and 'C' groups are also converging on the CANOCO Fragmented Sites axis 1, although this would not be expected due to the lack of correlation between this axis and distance/isolation factors (Section 7.5).

Figure 9.9: Hypothesised relationship between the critical thresholds of the species in this study and their observed changes in regional distribution (figure adapted from Wiens 1997).



9.7 ACADEMIC VERSUS APPLIED CONSERVATION: JOINED-UP GOVERNANCE

Butterfly ecology (as opposed to biology) is only a relatively recent area of study. Knowledge of grassland butterfly ecological requirements is still fairly poor although some of the scarcer species have been extensively researched recently (Oates 1995). Oates lists eight species where "comprehensive knowledge including management details" exists, four where "useful ecological knowledge, including management basics " exists,

eight where "basic knowledge, at least in some habitats or regions, including general understanding of habitat management" exists and five where "inadequate knowledge, especially regarding management" exists. He adds six species whose ecological requirements are almost unknown in detail, and these are the ubiquitous species: Essex skipper, large skipper, hedge brown, wall, ringlet and small heath. This study has hopefully added to our knowledge of these species' ecology in terms of habitat requirements and environmental preferences.

Ubiquity is no excuse for lack of input either. The wall brown has shown some alarming regional downward trends in recent decades, although a recovery is now apparent (Greatorex-Davies and Roy 2000). However, the small heath is showing some worrying long-term declines which are probably linked to the general 'well-being' of the British semi-natural grasslands, and this is the species about which Oates feels we know least of all.

Generally, the approach to nature conservation needs for British butterflies by the UK conservation agencies is 'bottom up' with the rarest and quickest declining being the subject of Species Action Plans under the Biodiversity Action Plan (*Biodiversity: the UK Steering Group Report, 1995*). However, only eleven species, of which six show strong associations with semi-natural grasslands, are subject to the highest tier, the Priority Action Plans. Several others have had Species Action Plans written for them by Butterfly Conservation (who also lead on the Priority species), where sufficient concern has been expressed over their status and decline. A good example is grizzled skipper (Brereton *et al* 1998). Among the research needs for this species, the following are listed: investigation of the dispersal ability, effect of habitat loss and isolation of colonies on population viability;

research on parasitoids and associated species in its habitats; investigation of the role of rabbit grazing in maintaining habitats and the extent of the species' reliance on rabbit grazing. This study will have added to the knowledge base on at least the last two fronts.

As flagship species, butterflies are ideal for driving nature conservation decision making. They are attractive, relatively easy to observe, and occupy a whole suite of habitats and seral stages within them. Managing for carefully selected butterfly communities should benefit a huge number of associated fauna and flora. While a systems based approach such as that proposed for chalk grassland invertebrates by Jones-Walters (1990) would be an ideal *modus operandi* for integrated nature conservation if resources were available, in reality, such careful management is still a long way off.

What is important, however, is that butterflies are viewed as indicators of certain conditions and are also seen as community members rather than as species existing in isolation. This study has hopefully moved research towards a more holistic approach to butterfly ecology.

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APPENDICES

APPENDIX 1a-d: Maps of NVC Types at Porton Down in 1991(from Wilson & Reed 1992)

a)

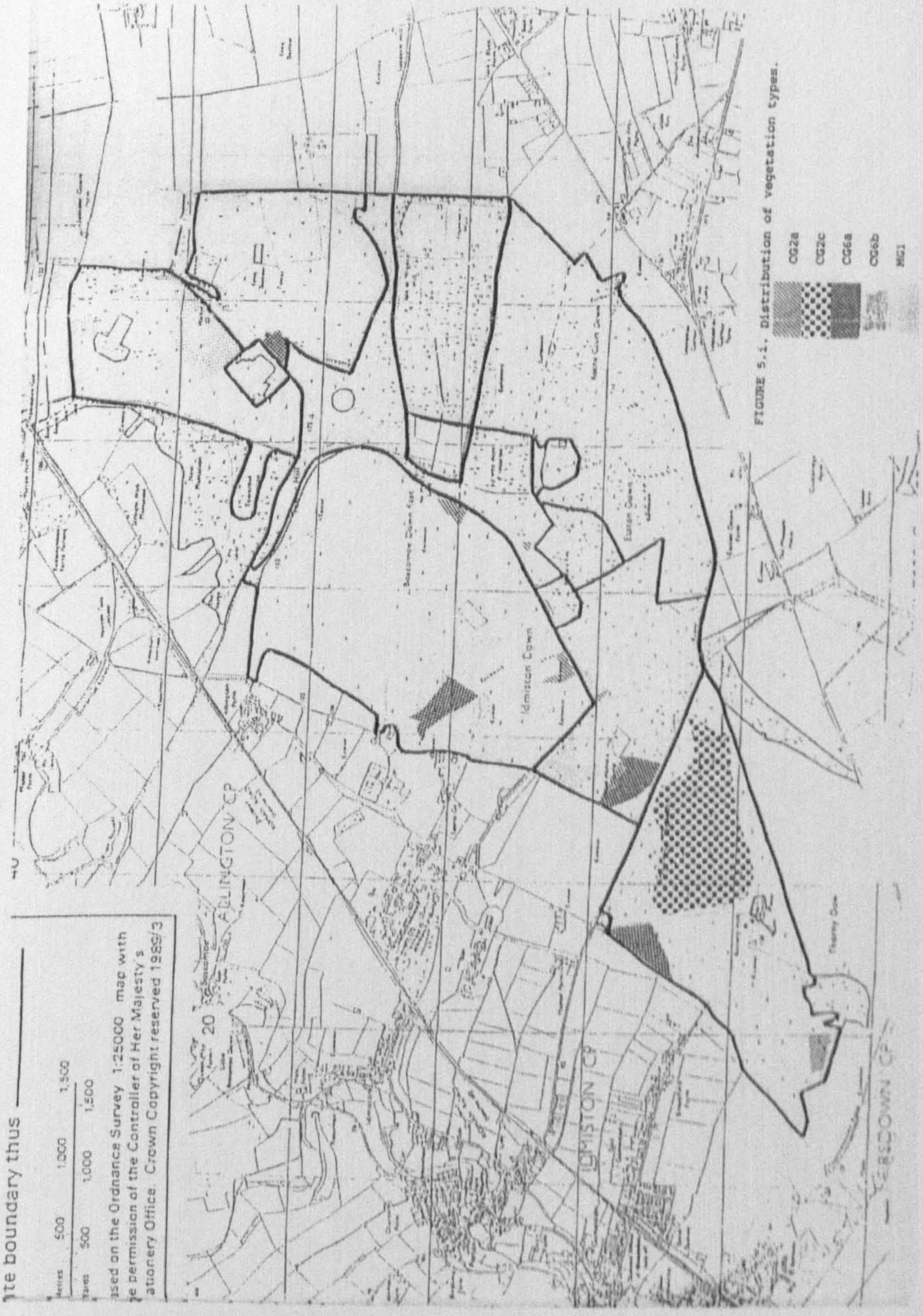

FIGURE 5.1. Distribution of vegetation types.

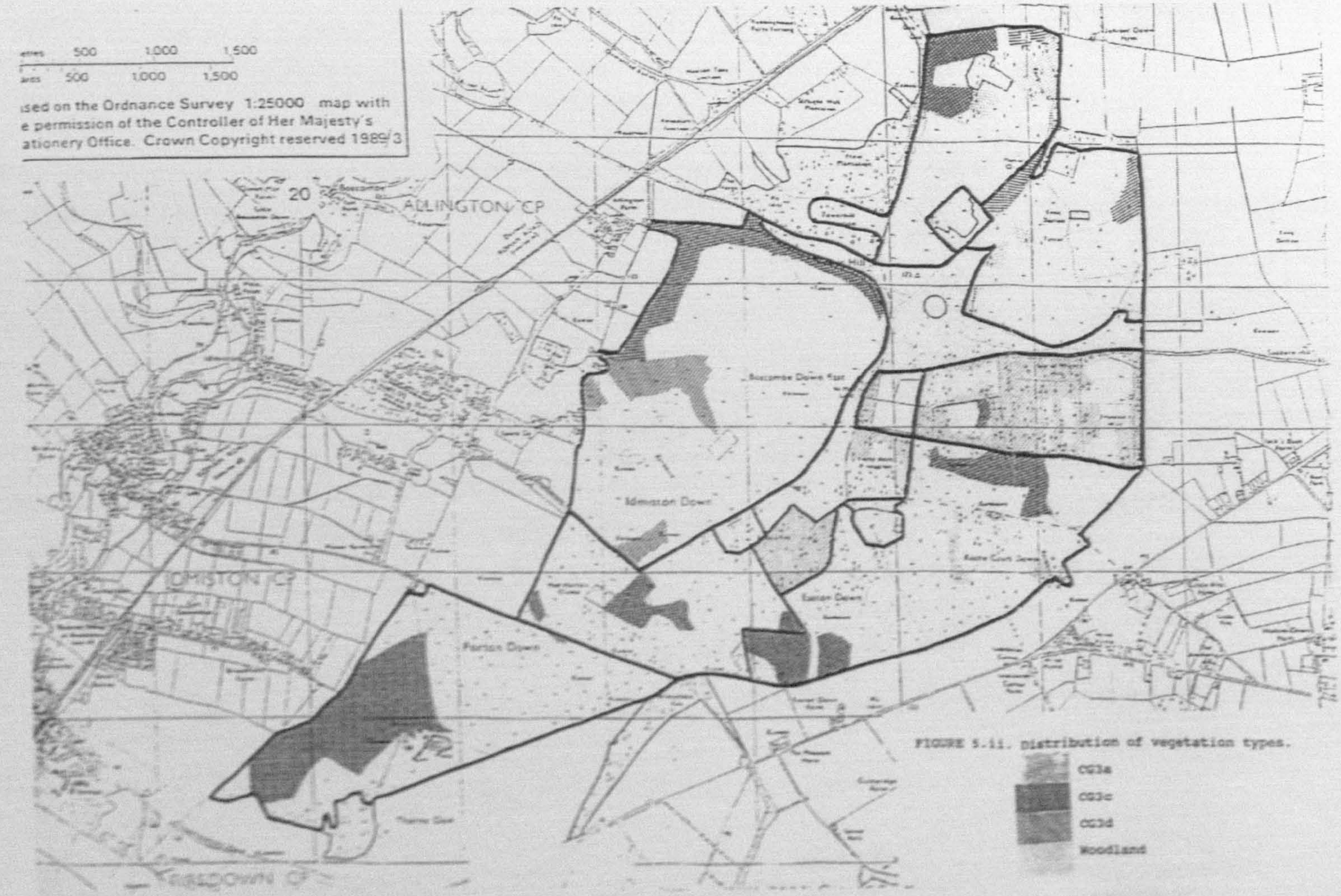

FIGURE 5.11. Distribution of vegetation types.

CG3a
CG3c
CG3d
Woodland

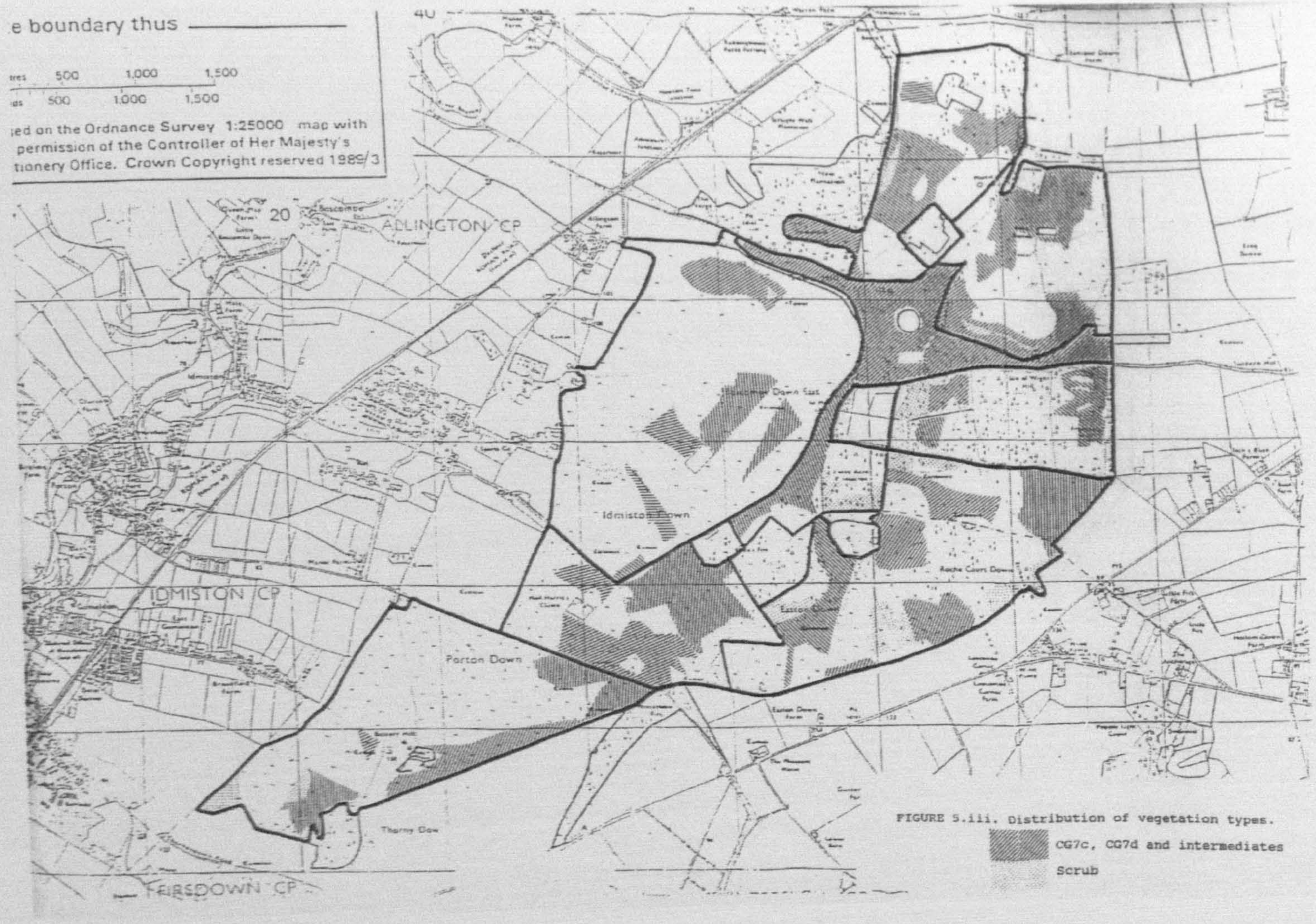

FIGURE 5.iii. Distribution of vegetation types.

CG7c, CG7d and intermediates

Scrub

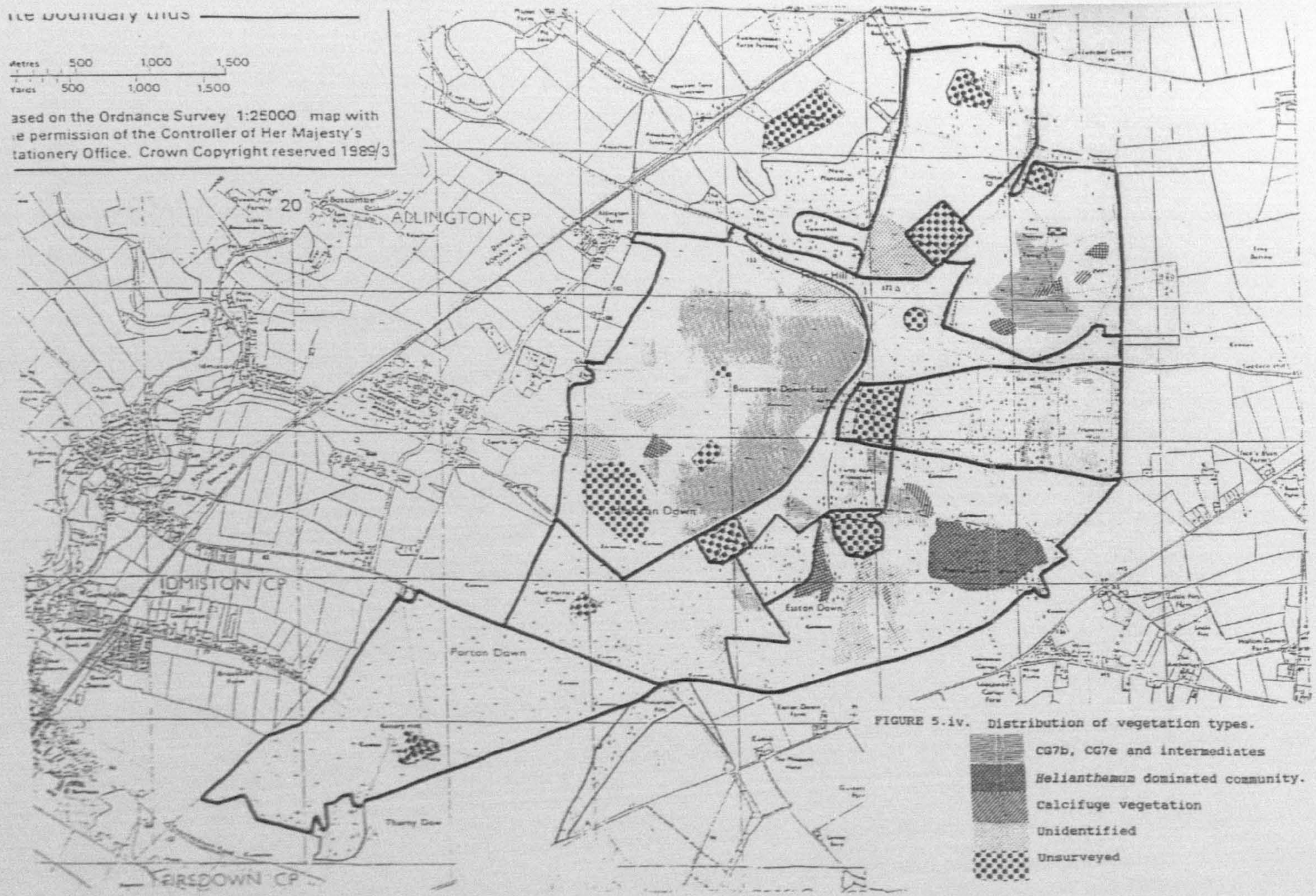

FIGURE 5.iv. Distribution of vegetation types.

- CG7b, CG7e and intermediates
- *Helianthemum* dominated community.
- Calcifuge vegetation
- Unidentified
- Unsurveyed

APPENDIX 2: Fragmented Sites Transect Data

Sites Surveyed in 1996

Site	Area (ha)	No. Transects	OS Grid Reference *
Porton Pheasant Fields:			
NW Corner	1.28	1	SU 2290 3495
'Long Strip'	0.15	1	SU 2305 3500
'Double Tumulus'	0.25	1	SU 2313 3495
Porton Field @ Gate 13	0.32	1	SU 2292 3472
Porton 'Clump'	0.75	1	SU 2244 3475
Winterslow Firs	4.6	2	SU 2198 3458
Porton area @ Gate 14/15	0.3	1	SU 2032 3369
Figsbury Ring & Mast Fld	12.3	7	SU 1888 3385
Thorneydown Tip Field	1.5	1	SU 2132 3437
Jowett's Clump	0.69	1	SU 2205 3390
Gutteridge's Farm	2.15	2	SU 2446 3438
Lopcombe Corner Farm	0.3	1	SU 2500 3503
Bracknell Croft	3.5	3	SU 1810 3308
Cockey & Laverstock Dns.	27.0	9	SU 1685 3150
King Manor Hill Palace	0.6	2	SU 1790 3005
King Manor Hill Bank	2.5	2	SU 1722 2967
Savage's Farm	1.2	2	SU 1865 3068
Witherington Down (E)	0.2	1	SU 2102 2471
Fussell's Lodge Road	0.3	2	SU 1930 3230
Stock's Bottom	0.6	1	SU 1978 1993
Pitton Downs:			
White Hill (S)	1.0	1	SU 2094 3067
White Hill (N)	1.35	1	SU 2118 3096
Barford Lane	3.0	3	SU 1918 2203

Pitton Downs:			
Blandford/Garvie	1.2	2	SU 2155 3153
Peartree Farm	1.2	1	SU 2192 3191
Bentleigh Farm	2.15	2	SU 2216 3214
Ashley's Copse	4.7	2	SU 2618 3474
Bussle's Wood	5.4	2	SU 2668 3451
Kestrel's Farm	0.4	1	SU 2744 3456
Broughton Down	42.7	10	SU 2850 3330
Barford Down	11.25	2	SU 2007 2282
Witherington Down (W)	6.7	2	SU 2055 2493
Pepperbox Hill	7.0	5	SU 2135 2480
Brickworth Down/Dean Hill	32.5	10	SU 2200 2555
Whitehouse Copse Ride	0.625	1	SU 2497 2600
Whitehouse Copse East	2.0	1	SU 2486 2584
RNAD:			
South	7.26	3	SU 2610 2645
Woodland Glade	0.23	1	SU 2603 2723
East Juniper Area	1.6	1	SU 2555 2733
North Banks	5.0	4	SU 2575 2647
Whitehouse Copse West	0.8	1	SU 2432 2589
Bullock's Hole	4.25	1	SU 2771 3421
	Total	99	

* Central site Grid reference

Sites Surveyed in 1997

Site	Area (ha)	No. Transects	OS Grid Reference *
Stockbottom Farm	0.12	1	SU 1958 3340
Jowett's East	4.34	2	SU 2284 3279
E. Winterslow Droveway	0.25	2	SU 2400 3388
Blanche's Field	3.92	2	SU 2555 3582
Haynes' Field	4.13	2	SU 2600 3547
Bussles Wood Droveway	0.19	1	SU 2709 3443
Broughton Down Extension	2.8	2	SU 2947 3267
Standlynch Down	0.21	3	SU 2035 2422
Witherington Dn. Reservoir	0.06	2	SU 2066 2417
Cockey Dn. Footpath	0.12	1	SU 1721 3261
Thorneydown Dual C'way	0.91	4	SU 2124 3400
Bossington	4.69	3	SU 3213 3120
Total		25	

APPENDIX 3: Recording Forms Used for Botanical and Associated Habitat and Environmental Variables. (Following Two Pages)

Grassland card 2: community/quadrat

ENGLISH NATURE

April 1994

Surveyors

Is this a community ☐ **or a quadrat** ☐

Survey title

Site name

Site Grid Reference **Date of survey**

Community name

Surveyors CO/QU code no. (from map) **CO/QU Grid Ref**

Computer input reference **Quadrat no.**

Community/quadrat area **(ha) for community; (sq m) for quadrat**

Slope ° - ° **Soil depth (cm)**

Aspect ° - ° **pH**

Vegetation height (cm) - **(Ignore extreme variation)**

Photographic record **(No. of exposures)**

(Where held)

Community/quadrat description and assessment

Notes on management activities (including grazers, management etc. not listed in key-words). Note any difference in management of compartments if the community extends over more than one compartment.

Community records only

Management key-words

Grazing intensity		
Heavy	HV	
Light	LT	
Moderate	MO	
None	NO	
Over	OG	
Under	UN	
Unknown	X	

Grazers		
Cattle	CT	
Deer	DE	
Horse/donkey	HO	
None	NO	
Rabbit	RA	
Sheep	SH	
Unknown	X	
Wildfowl	WF	

Other management		
Artificial fertilisers	AF	
Bracken control	BC	
Burning	BU	
Drain/ditch	DM	
Farmyard manure	FM	
Hay	HA	
Lime	LM	
Mowing/topping	MT	
None	NO	
Noxious weed control	NC	
Scrub control	SC	
Silage	SI	
Slurry/other manure	SM	
Stock feeding	SF	
Unknown	X	

Features		
Anthills	AN	
Archeological remains	AH	
Flooding	FL	
Molehills	MH	
None	NO	
Poaching	PO	
Ridge and furrow	RF	
Unknown	X	

SITE/COMM/QUAD ID

	W/D	L	+	
120				Agrostis canina
123				capill
122				stolon
2701				vinea
124				Aira caryoph
125				praecox
156				Alopecurus geo
158				pra
171				Anthoxan odor
197				Arrhenath elat
655				Avenula pra
656				pub
246				Brachypod pina
247				sylv
251				Briza media
254				Bromus comm
256				erectus
258				hord
460				Cynosurus cris
465				Dactylis glom
1249				Danthonia dec
477				Deschamp cesp
478				flex
369				Deamazeria rig
118				Elymus repens
572				Festuca arundin
574				ovina
575				pratens
576				rubra
639				Glyceria fluitans
680				Holcus lanatus
685				Hordeum secal
746				Koeleria macras
796				Lolium perenne
876				Molinia caerulea
900				Nardus stricta
959				Phleum bertol
960				pratense
981				Poa annua
988				pratensis
989				subcaerulea
990				trivialis
1245				Sesleria albicans
1356				Trisetum flav
104				Achillea mill
105				ptarm
113				Agrimonia eup
127				Ajuga reptans
131				Alchemilla filic
132				glab
141				xanth
152				Allium vineale
160				Anacamptis pyr
163				Anagallis tenella
167				Angelica sylvest
168				Antennaria dio
173				Anthriscus sylv
174				Anthyllis vulner
177				Aphanes arven
185				Arabis hirsuta
194				Arenaria serpyll
202				Asperula cynan
212				Astragalus danic
230				Bellis perennis
2802				Bervis sp
241				Blackstonia perf
278				Calluna vulgaris
279				Caltha palustris
284				Campanula glom
288				rot
292				Cardamine flex
295				pra
299				Carduus nutans
301				Carex acuta
302				acutiform
308				binervis
310				caryophyll
312				demissa
313				flacca
316				glauca
317				diandra
319				echinata
321				flacca

	W/D	L	+	
324				Carex hirta
325				hostiana
2817				humilis
329				lepidocarp
333				nigra
336				otrubae
337				ovalis
338				pallescens
339				panicea
364				pilulifera
347				pulicaris
356				spicata *
362				Carlina vulgaris
365				Carum verticill
371				Centaurea nigra
372				scab
373				Centaurium eryt
380				Cerastium arven
384				font
383				glom
391				Chamerion ang
2687				Cirsium acaule
415				arvense
2714				dissect
416				erioph
417				helen
418				palustre
419				vulgare
422				Chenopodium vul
428				Cochlearia var
429				Colchicum aut
431				Conopodium maj
433				Convolvulus arv
2983				Cornus sanguinea
2611				Crataegus mono
447				Crepis capillaris
449				paludosa
459				Cynoglossum off
466				Dactylorh fuch
467				incarn
468				macul
469				praet
470				purp
475				Daucus carota
481				Dianthus delt
482				Digitalis purp
494				Drosera rotund
504				Echium vulgare
509				Epilobium hirsut
511				palust
521				parvif
525				Equisetum arv
526				fluv
532				pal
533				sylv
535				Erica cinerea
537				tetralix
541				Eriophorum ang
542				Erodium cicut
546				Eupatorium cann
549				Euphrasia sp
558				Filipendula ulm
568				vulg
583				Fragaria vesca
584				Galium hercyn
587				boreale
605				cruciata
606				mollugo
435				palustre
607				parisie
609				sterneri
610				uliginos
611				verum
612				Genista anglica
613				tinctoria
614				Gentianella amar
615				camp
619				Geranium dissect
620				molle
622				pratense

	W/D	L	+	
968				Geranium robert
970				sylvat
973				Geum rivale
974				urbanum
975				Glechoma heder
976				Gymnadenia conn
977				Helianth numm
978				Heracleum sphon
1203				Hieracium pilos
994				Hypochoeris radi
995				Hyacinth non scr
998				Hydrocotyle vulg
1000				Hypericum humif
1004				perf
1043				pulch
1046				tetrap
1049				Hypochoeris rad
1050				Inula conyza
1051				Iris pseudacorus
1052				Isolepis setacea
1054				Juncus acutiflor
1053				articulus
1056				bufonius
1058				bulbosus
1059				conglom
2624				effusus
1066				inflexus
1069				squarros
2939				subnodul
1081				Knautia arvensis
1088				Lathyrus montan
1089				nisseolia
1093				pratensis
1106				Leontodon autum
1136				hispid
1139				taras
1140				Leucanthem vulgm
1142				Linum catharti
1143				Lonicera periclym
1163				Lotus corniculat
1167				Lysimach nemo
1159				Lysimachia vulgaris
1158				Lythrum salicaria
2729				Medicago lupulina
1179				Menyanthes trifol
1185				Mentha aquatica
1193				arvensis
1195				Myosotis arvensis
1227				discolor
1233				laxa
1236				nemorosa
1237				scorp
2921				secunda
1239				Narthecium ossif
1244				Odontites verna
1247				Omalotheca sylvat
1250				supina
1259				Onobrychis viciif
1272				Ononis repens
1273				spinosa
334				Orthotrichum rup
1292				Osmunda regalis
1282				Oxalis acetosella
1288				corniculata
1289				europaea
1290				Oxyria digyna
1291				Parnassia palust
1333				Pedicularis palust
1334				sylvat
1347				Phyteuma tener
1333				Picris echioides
1248				hieracioides
1339				Plantago coronop

	W/D	L	+	
1340				Plantago lanceol
1341				major
1342				maritima
1343				media
1344				Platanthera bifol
1345				chlor
1346				Polygala calcarea
1347				serpyllif
1375				vulgaris
1381				Polygonum amph
1381				bistor
1389				hydrop
1391				Potentilla anserin
1394				erecta
1395				palust
1396				reptans
1401				sterilis
1400				tormen
1404				Prunella lacinata
2997				vulgaris
1411				Pteridium aquilin
1412				Pyrola rotundif
2707				Ranunculus acris
1416				bulbosus
1418				flammula
1422				Rhamnus cath
1423				frang
1427				pumil
1429				Rosa
1497				Rhinanthus min
1318				Rubus fruticos
1319				Rumex acetosa
1321				acetosella
1346				crispus
1445				obtusif
1321				Salix aurita
1377				fragilis
1393				repens
1430				Salix viminalis
1438				repens
1849				Salvia verbenaca
1477				Sanguisorba min
1482				offici
1483				Saxifraga granul
1484				granul
1488				Scabiosa columb
1497				Scorzonera humil
1498				Selaginella sel
1499				Senecio aquatic
1500				erucifol
1501				jacobaea
1502				sylvat
1503				Silaum silaus
1504				Silene vulgaris
1505				Solanum nigr
1506				dulcam
1507				Solidago virgaur
1508				Sorbus aucup
1509				Succisa pratens
1510				Taraxacum sp
1511				Teucrium scorod
1512				Thalictrum flav
				minus
1				Thymus bracteat
1				Thymus praecox
1				polyt
1				Tormentilla erec
1				Trifolium arvense

	W/D	L	+	
1510				Trifolium ornith
1511				Trifolium arvense
1512				ours
1513				dubium
1514				fragif
1515				glomer
1516				pra
1517				repens
1518				scab
1519				Trollius europ
1520				Ulex europaeus
1521				gallii
1522				Urtica dioica
1523				Vaccinium myrt
1524				Valeriana dioica
1525				officin
1526				Verbena offic
1527				Veronica arvensis
1528				beccab
1529				chamae
1530				officin
1531				scutel
1532				serpyll
1533				Viburnum lant
1534				Vicia cracca
1535				lathy
1536				lutea
1537				sativa
1538				sylvatica
1539				Viola canina
1540				palus
1541				riviniana
1542				Zygiella x-not
1487				Achillea mill
1318				Aconitum napel
1319				Actaea spicata
1321				Aegopodium pod
1346				Agrostis gigant
1445				stolon
1321				Alchemilla alpina
1377				Allium ursinum
1393				Anemone nemor
1430				Angelica sylvest
1438				Anthriscus sylv
1849				Arctium minus
1477				Arrhenath elat
1482				Artemisia vulg
1483				Asplenium scol
1484				Athyrium filix
1488				Bellis perennis
1497				Betula pubesc
1498				Brachypod sylv
1499				Bromus ramos
1500				Calamagr epig
1501				Calystegia sepi
1502				Campanula lati
1503				Cardamine flex
1504				Carex pendula
1505				Centaurea nigr
1506				Cerastium holo
1507				Chaerophyll temul
1508				Circaea lutet
1509				Cirsium palust
1510				Corylus avell
1511				Crataegus monog
1512				Cystopteris fragil
1513				Dactylis glom
1514				Dactylorh fuch
1515				Deschamp cesp
1516				Digitalis purp
1517				Dryopteris aemul
1518				dilat
1519				filix-mas
1520				Epilobium hirsut
1521				montan
1522				Equisetum arv
1523				fluv
1524				hyem
1525				pal
1526				sylv
1527				Euonymus europ
1528				Eupatorium cann
1529				Fagus sylvat
1530				Festuca gigant
1531				rubra
1532				Filipendula ulm
1533				Fragaria vesca
1534				Galeopsis tetra
1535				Galium aparine
1536				odorat
1537				palust
1538				saxatile
1539				verum
1540				Geranium robert
1541				Geum urbanum
1542				Glechoma heder

Additional Species

W = DAFOR cover for whole stand D = DOMIN cover for quadrat L = DAFOR cover for local variation in abundance in stand + = present

ZOMEN 91-1987 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3-2224-2225-2226-2227-2228-2229-2230-2231-2232-2233-2234-2235-2236-2237-2238-2239-2240-2241-2242-2243-2244-2245-2246-2247-2248-2249-2250-2251-2252-2253-2254-2255-2256-2257-2258-2259-2260-2261-2262-2263-2264-2265-2266-2267-2268-2269-2270-2271-2272-2273-2274-2275-2276-2277-2278-2279-2280-2281-2282-2283-2284-2285-2286-2287-2288-2289-2290-2291-2292-2293-2294-2295-2296-2297-2298-2299-2300-2301-2302-2303-2304-2305-2306-2307-2308-2309-2310-2311-2312-2313-2314-2315-2316-2317-2318-2319-2320-2321-2322-2323-2324-2325-2326-2327-2328-2329-2330-2331-2332-2333-2334-2335-2336-2337-2338-2339-2340-2341-2342-2343-2344-2345-2346-2347-2348-2349-2350-2351-2352-2353-2354-2355-2356-2357-2358-2359-2360-2361-2362-2363-2364-2365-2366-2367-2368-2369-2370-2371-2372-2373-2374-2375-2376-2377-2378-2379-2380-2381-2382-2383-2384-2385-2386-2387-2388-2389-2390-2391-2392-2393-2394-2395-2396-2397-2398-2399-2400-2401-2402-2403-2404-2405-2406-2407-2408-2409-2410-2411-2412-2413-2414-2415-2416-2417-2418-2419-2420-2421-2422-2423-2424-2425-2426-2427-2428-2429-2430-2431-2432-2433-2434-2435-2436-2437-2438-2439-2440-2441-2442-2443-2444-2445-2446-2447-2448-2449-2450-2451-2452-2453-2454-2455-2456-2457-2458-2459-2460-2461-2462-2463-2464-2465-2466-2467-2468-2469-2470-2471-2472-2473-2474-2475-2476-2477-2478-2479-2480-2481-2482-2483-2484-2485-2486-2487-2488-2489-2490-2491-2492-2493-2494-2495-2496-2497-2498-2499-2500-2501-2502-2503-2504-2505-2506-2507-2508-2509-2510-2511-2512-2513-2514-2515-2516-2517-2518-2519-2520-2521-2522-2523-2524-2525-2526-2527-2528-2529-2530-2531-2532-2533-2534-2535-2536-2537-2538-2539-2540-2541-2542-2543-2544-2545-2546-2547-2548-2549-2550-2551-2552-2553-2554-2555-2556-2557-2558-2559-2560-2561-2562-2563-2564-2565-2566-2567-2568-2569-2570-2571-2572-2573-2574-2575-2576-2577-2578-2579-2580-2581-2582-2583-2584-2585-2586-2587-2588-2589-2590-2591-2592-2593-2594-2595-2596-2597-2598-2599-2600-2601-2602-2603-2604-2605-2606-2607-2608-2609-2610-2611-2612-2613-2614-2615-2616-2617-2618-2619-2620-2621-2622-2623-2624-2625-2626-2627-2628-2629-2630-2631-2632-2633-2634-2635-2636-2637-2638-2639-2640-2641-2642-2643-2644-2645-2646-2647-2648-2649-2650-2651-2652-2653-2654-2655-2656-2657-2658-2659-2660-2661-2662-2663-2664-2665-2666-2667-2668-2669-2670-2671-2672-2673-2674-2675-2676-2677-2678-2679-2680-2681-2682-2683-2684-2685-2686-2687-2688-2689-2690-2691-2692-2693-2694-2695-2696-2697-2698-2699-2700-2701-2702-2703-2704-2705-2706-2707-2708-2709-2710-2711-2712-2713-2714-2715-2716-2717-2718-2719-2720-2721-2722-2723-2724-2725-2726-2727-2728-2729-2730-2731-2732-2733-2734-2735-2736-2737-2738-2739-2740-2741-2742-2743-2744-2745-2746-2747-2748-2749-2750-2751-2752-2753-2754-2755-2756-2757-2758-2759-2760-2761-2762-2763-2764-2765-2766-2767-2768-2769-2770-2771-2772-2773-2774-2775-2776-2777-2778-2779-2780-2781-2782-2783-2784-2785-2786-2787-2788-2789-2790-2791-2792-2793-2794-2795-2796-2797-2798-2799-2800-2801-2802-2803-2804-2805-2806-2807-2808-2809-2810-2811-2812-2813-2814-2815-2816-2817-2818-2819-2820-2821-2822-2823-2824-2825-2826-2827-2828-2829-2830-2831-2832-2833-2834-2835-2836-2837-2838-2839-2840-2841-2842-2843-2844-2845-2846-2847-2848-2849-2850-2851-2852-2853-2854-2855-2856-2857-2858-2859-2860-2861-2862-2863-2864-2865-2866-2867-2868-2869-2870-2871-2872-2873-2874-2875-2876-2877-2878-2879-2880-2881-2882-2883-2884-2885-2886-2887-2888-2889-2890-2891-2892-2893-2894-2895-2896-2897-2898-2899-2900-2901-2902-2903-2904-2905-2906-2907-2908-2909-2910-2911-2912-2913-2914-2915-2916-2917-2918-2919-2920-2921-2922-2923-2924-2925-2926-2927-2928-2929-2930-2931-2932-2933-2934-2935-2936-2937-2938-2939-2940-2941-2942-2943-2944-2945-2946-2947-2948-2949-2950-2951-2952-2953-2954-2955-2956-2957-2958-2959-2960-2961-2962-2963-2964-2965-2966-2967-2968-2969-2970-2971-2972-2973-2974-2975-2976-2977-2978-2979-2980-2981-2982-2983-2984-2985-2986-2987-2988-2989-2990-2991-2992-2993-2994-2995-2996-2997-2998-2999-3000-3001-3002-3003-3004-3005-3006-3007-3008-3009-3010-3011-3012-3013-3014-3015-3016-3017-3018-3019-3020-3021-3022-3023-3024-3025-3026-3027-3028-3029-3030-3031-3032-3033-3034-3035-3036-3037-3038-3039-3040-3041-3042-3043-3044-3045-3046-3047-3048-3049-3050-3051-3052-3053-3054-3055-3056-3057-3058-3059-3060-3061-3062-3063-3064-3065-3066-3067-3068-3069-3070-3071-3072-3073-3074-3075-3076-3077-3078-3079-3080-3081-3082-3083-3084-3085-3086-3087-3088-3089-3090-3091-3092-3093-3094-3095-3096-3097-3098-3099-3100-3101-3102-3103-3104-3105-3106-3107-3108-3109-3110-3111-3112-3113-3114-3115-3116-3117-3118-3119-3120-3121-3122-3123-3124-3125-3126-3127-3128-3129-3130-3131-3132-3133-3134-3135-3136-3137-3138-3139-3140-3141-3142-3143-3144-3145-3146-3147-3148-3149-3150-3151-3152-3153-3154-3155-3156-3157-3158-3159-3160-3161-3162-3163-3164-3165-3166-3167-3168-3169-3170-3171-3172-3173-3174-3175-3176-3177-3178-3179-3180-3181-3182-3183-3184-3185-3186-3187-3188-3189-3190-3191-3192-3193-3194-3195-3196-3197-3198-3199-3200-3201-3202-3203-3204-3205-3206-3207-3208-3209-3210-3211-3212-3213-3214-3215-3216-3217-3218-3219-3220-3221-3222-322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APPENDIX 4: Form Used For Recording Rabbit Fecal Counts and Sward Height at Quadrat Locations

Area: _____ Date: _____

Quadrat Number	Location	Rabbit fecal counts 1x1m<8d	1x1mTot	2x2m<8d	2x2m Tot	Sward height (cm) 1	2	3	4	5

APPENDIX 5: Preferred Larval Food-plants

Butterfly Species	Larval Food-plant
Small skipper	Yorkshire fog *Holcus lanatus*, cock's-foot *Dactylis glomerata*, wood false-brome *Brachypodium sylvaticum*.
Essex skipper	Cock's-foot *Dactylis glomerata*, wood false-brome *Brachypodium sylvaticum*.
Silver-spotted skipper	Sheep's fescue *Festuca ovina*.
Large skipper	Cock's-foot *Dactylis glomerata*, wood false-brome *Brachypodium sylvaticum*.
Dingy skipper	Bird's-foot trefoil *Lotus corniculatus*, horse-shoe vetch *Hippocrepis commosa*.
Grizzled skipper	Wild strawberry *Fragaria vesca*.
Green hairstreak	Common rock-rose *Helianthemum nummularium*, bird's-foot trefoil *Lotus corniculatus*, dogwood *Cornus sanguineus*, buckthorn *Rhamnus cathartica*.
Small copper	Sorrel *Rumex acetosa*, sheep's sorrel *R. acetosella*.
Small blue	Kidney vetch *Anthyllis vulneraria*.
Brown argus	Common rock-rose *Helianthemum nummularium*.
Common blue	Bird's-foot trefoil *Lotus corniculatus*, black medick *Medicago lupulina*, red clover *Trifolium pratense*, white clover *Trifolium repens*.

Chalkhill blue	Horse-shoe vetch *Hippocrepis commosa*.
Dark green fritillary	Hairy violet *Viola hirta*.
Marbled white	Various grass Graminae species (see Section 2.4.2).
Hedge brown	Fescues *Festuca* spp., bents *Agrostis* spp., sweet vernal-grass *Anthoxanthum odoratum*.
Meadow brown	Various grass Graminae species (see Section 2.4.2).
Ringlet	Cock's-foot *Dactylis glomerata*, wood false-brome *Brachypodium sylvaticum*, smooth meadow grass *Poa pratensis*, couch grass *Elymus repens*.
Small heath	Fescues *Festuca* spp., bents *Agrostis* spp., smooth meadow grass *Poa pratensis*.

APPENDIX 6: Preferred Adult Butterfly Nectar Sources

Butterfly Species	Nectar Species
Small skipper	Bramble *Rubus fruticosus agg.*, common ragwort *Senecio jacobaea*, knapweeds *Centaurea* spp., field scabious *Knautia arvensis*, marjoram *Origanum vulgare*, common fleabane *Pulicaria dysenterica*, selfheal *Prunella vulgaris*, betony *Betonica officinalis*, red clover *Trifolium pratense*, vetches *Vicia* spp., bird's-foot trefoil *Lotus corniculatus*, thistles *Cirsium* spp., devil's-bit scabious *Succis pratensis*, musk thistle *Carduus nutans*.
Essex skipper	Knapweeds *Centaurea* spp., heather *Calluna vulgaris*, common fleabane *Pulicaria dysenterica*, dandelion *Taraxacum officinale agg.*, selfheal *Prunella vulgaris*, hawkweeds *Hieracium* spp., red clover *Trifolium pratense*, white clover *Trifolium repens*, thistles *Cirsium* spp. (partic. creeping thistle *C. arvense*), small scabious *Scabiosa columbaria*.
Silver-spotted skipper	Dwarf thistle *Cirsium acaule*, carline thistle *Carlina vulgaris*, knapweeds *Centaurea* spp., hawkweeds *Hieracium* spp., field scabious *Knautia arvensis*, autumn gentian *Gentianella amarella*, (shrubs).
Large skipper	Bramble *Rubus fruticosus agg.*, wild privet *Ligustrum vulgare*, knapweeds *Centaurea* spp., field scabious *Knautia arvensis*, dandelion *Taraxacum officinale agg.*, kidney vetch *Anthyllis vulneraria*, vetches *Vicia* spp., bird's-foot trefoil *Lotus corniculatus*, thistles *Cirsium* spp., devil's-bit scabious *Succis pratensis*, musk thistle *Carduus nutans*, sainfoin *Onobrychis viciifolia*.

Dingy skipper	Buttercups *Ranunculus* spp., hawkweeds *Hieracium* spp., vetches *Vicia* spp., bird's-foot trefoil *Lotus corniculatus*, horse-shoe vetch *Hippocrepis comosa*, milkworts *Polygala* spp., fragrant orchid *Gymnadenia conopsea*.
Grizzled skipper	Buttercups *Ranunculus* spp., bird's-foot trefoil *Lotus corniculatus*.
Green hairstreak	Wild privet *Ligustrum vulgare*, hawkweeds *Hieracium* spp., bird's-foot trefoil *Lotus corniculatus*, wayfaring tree *Viburnum lantana* (flowers and honeydew), common rock-rose *Helianthemum nummularium*, milkworts *Polygala* spp., germander speedwell *Veronica chamaedrys*.
Small copper	Buttercups *Ranunculus* spp., daisy *Bellis perennis*, yarrow *Achillea millefolium*, common ragwort *Senecio jacobaea*, heather *Calluna vulgaris*, common fleabane *Pulicaria dysenterica*, dandelion *Taraxacum officinale agg.*, hawkweeds *Hieracium* spp., red clover *Trifolium pratense*, thistles *Cirsium* spp., knapweeds *Centaurea* spp., musk thistle *Carduus nutans*, hemp agrimony *Eupatorium cannabinum*, marjoram *Origanum vulgare*.
Small blue	Kidney vetch *Anthyllis vulneraria*, vetches *Vicia* spp., bird's-foot trefoil *Lotus corniculatus*, red clover *Trifolium pratense*, white clover *Trifolium repens*.
Brown argus	Wild thyme *Thymus praecox arcticus*, common ragwort *Senecio jacobaea*, marjoram *Origanum vulgare*, hawkweeds *Hieracium* spp., white clover *Trifolium repens*, milkworts *Polygala* spp..

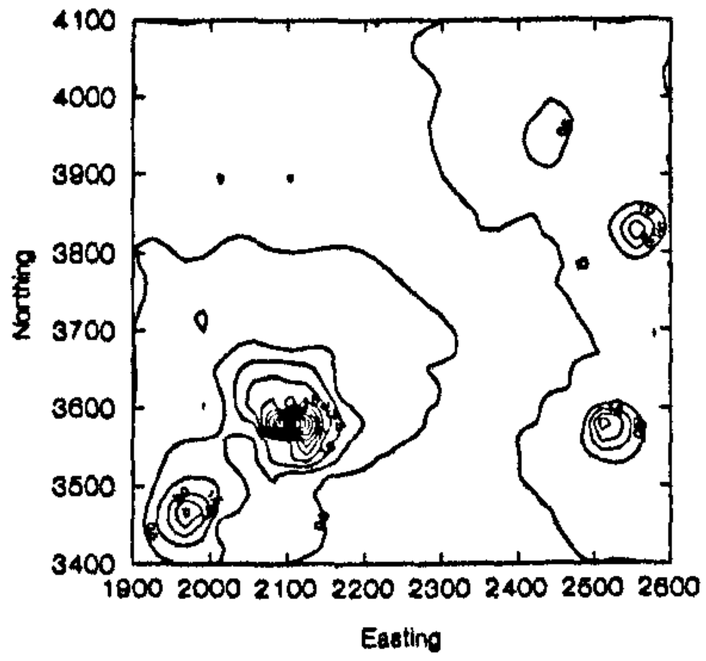
Common blue	Buttercups *Ranunculus* spp., wild thyme *Thymus praecox arcticus*, common ragwort *Senecio jacobaea*, knapweeds *Centaurea* spp., field scabious *Knautia arvensis*, marjoram *Origanum vulgare*, carline thistle *Carlina vulgaris*, common fleabane *Pulicaria dysenterica*, white clover *Trifolium repens*, Kidney vetch *Anthyllis vulneraria*, vetches *Vicia* spp., bird's-foot trefoil *Lotus corniculatus*, thistles *Cirsium* spp..
Chalkhill blue	Wild thyme *Thymus praecox arcticus*, field scabious *Knautia arvensis*, marjoram *Origanum vulgare*, carline thistle *Carlina vulgaris*, selfheal *Prunella vulgaris*, bird's-foot trefoil *Lotus corniculatus*, thistles *Cirsium* spp., eyebrights *Euphrasia* spp..
Dark green fritillary	Knapweeds *Centaurea* spp., field scabious *Knautia arvensis*, , thistles *Cirsium* spp., musk thistle *Carduus nutans*.
Marbled white	Bramble *Rubus fruticosus agg.*, wild privet *Ligustrum vulgare*, knapweeds *Centaurea* spp., marjoram *Origanum vulgare*, thistles *Cirsium* spp., musk thistle *Carduus nutans*, pyramidal orchid *Anacamptis pyramidalis*.
Hedge brown	Bramble *Rubus fruticosus agg.*, common ragwort *Senecio jacobaea*, field scabious *Knautia arvensis*, marjoram *Origanum vulgare*, carline thistle *Carlina vulgaris*, common fleabane *Pulicaria dysenterica*, thistles *Cirsium* spp., musk thistle *Carduus nutans*.
Meadow brown	Bramble *Rubus fruticosus agg.*, wild privet *Ligustrum vulgare*, knapweeds *Centaurea* spp., marjoram *Origanum vulgare*, field scabious *Knautia arvensis*, devil's-bit scabious *Succis pratensis*.
Ringlet	Bramble *Rubus fruticosus agg.*, wild privet *Ligustrum vulgare*, marjoram *Origanum vulgare*, thistles *Cirsium* spp., musk thistle *Carduus nutans*.

Small heath	Buttercups *Ranunculus* spp., wild thyme *Thymus praecox arcticus*, hawkweeds *Hieracium* spp., hemp agrimony *Eupatorium cannabinum*, marjoram *Origanum vulgare*.

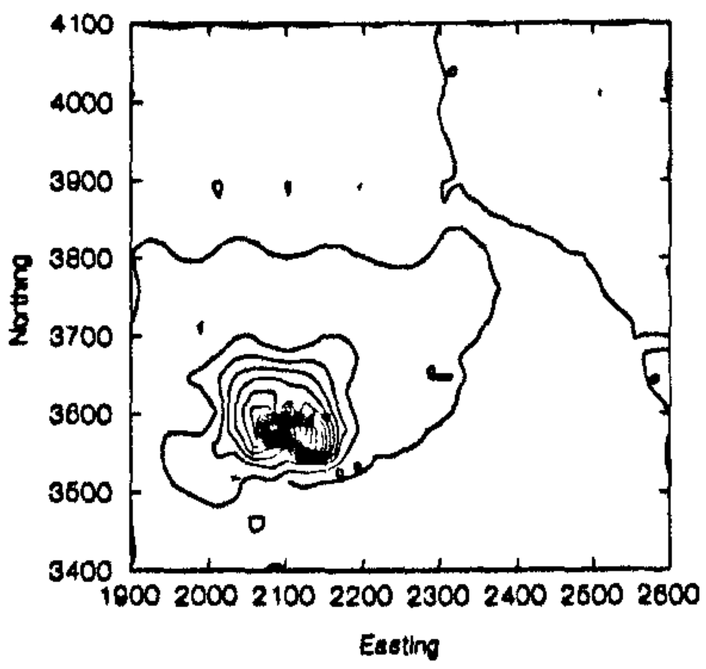
APPENDIX 7: NEXPO Density Contour Maps of Species on Porton Down

Refer to Figure 2.2 for data source points.

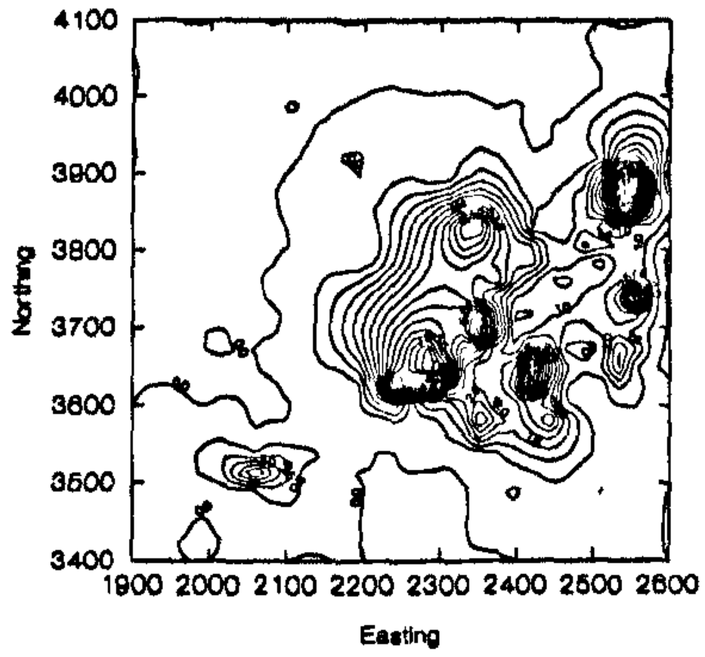
Small skipper 1995



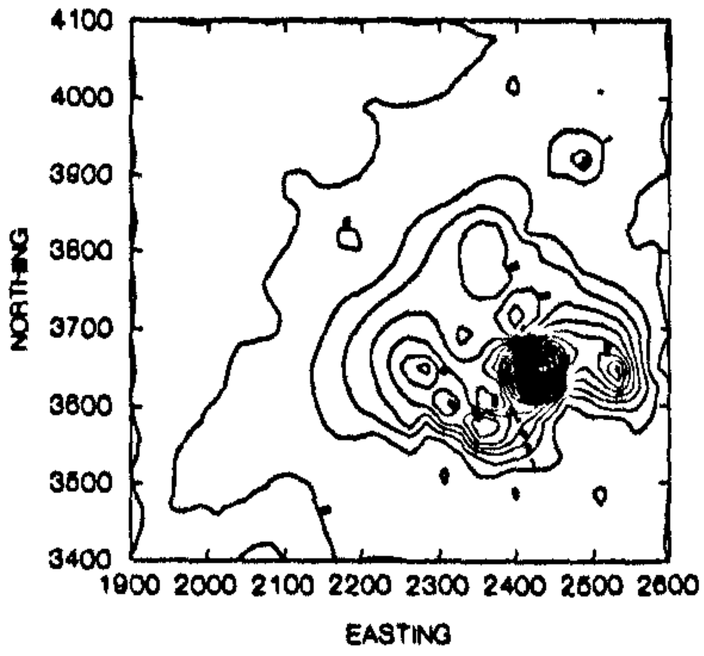
Essex skipper 1995



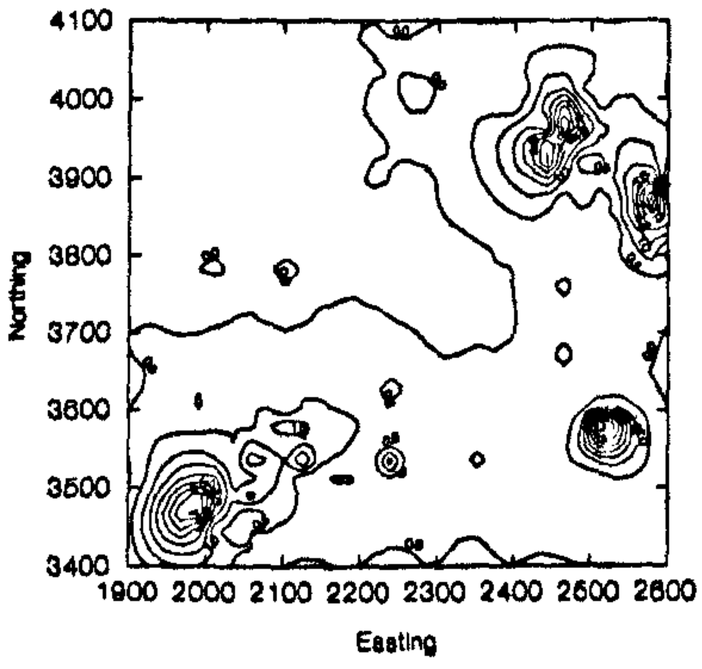
Silver-spotted skipper 1995



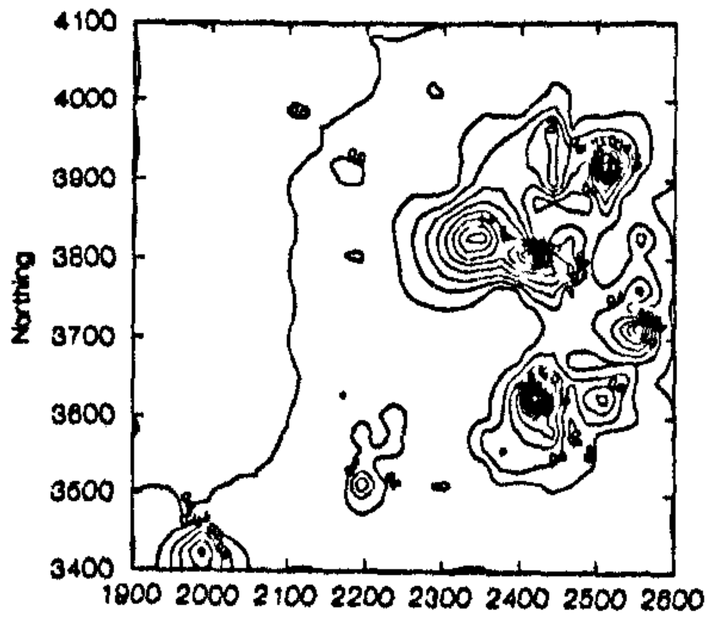
Silver-spotted skipper 1997



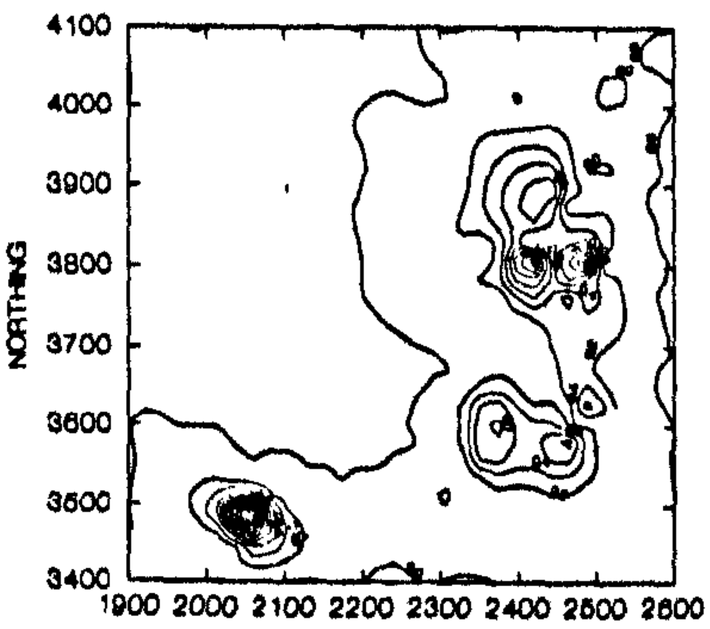
Large skipper 1995



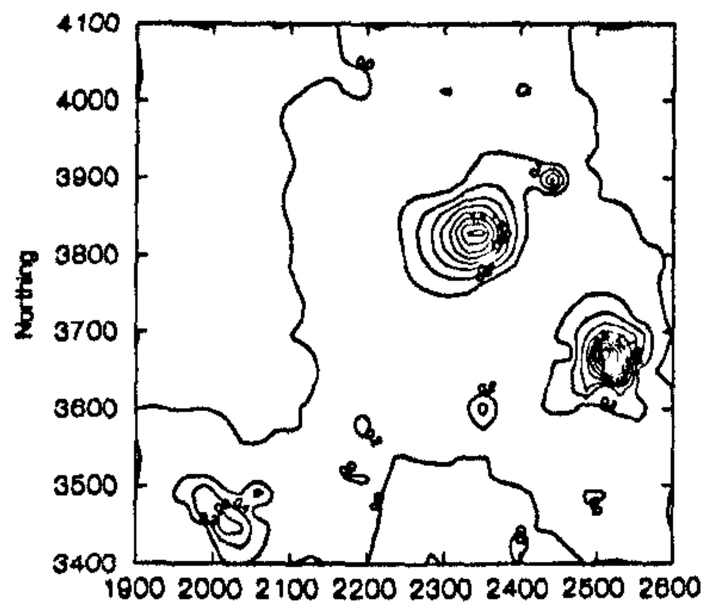
Dingy skipper 1995



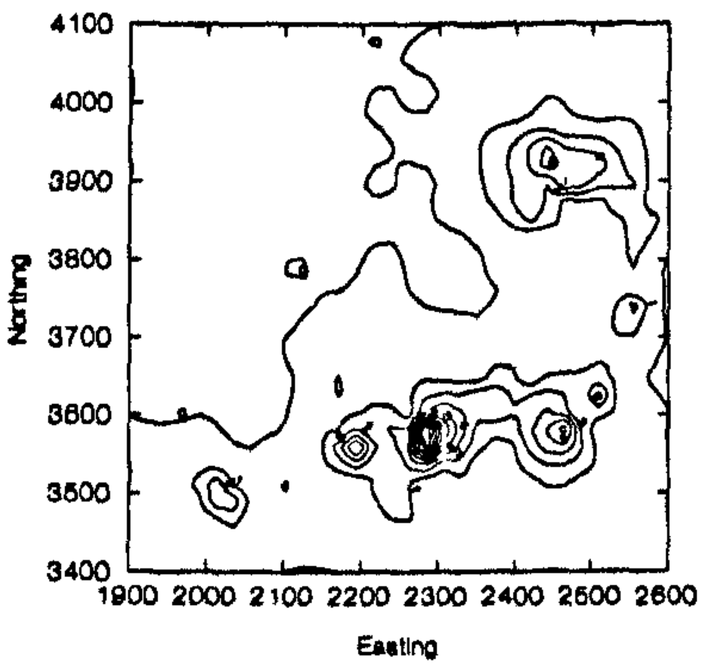
Dingy skipper 1997



Grizzled skipper 1995



Green hairstreak 1995



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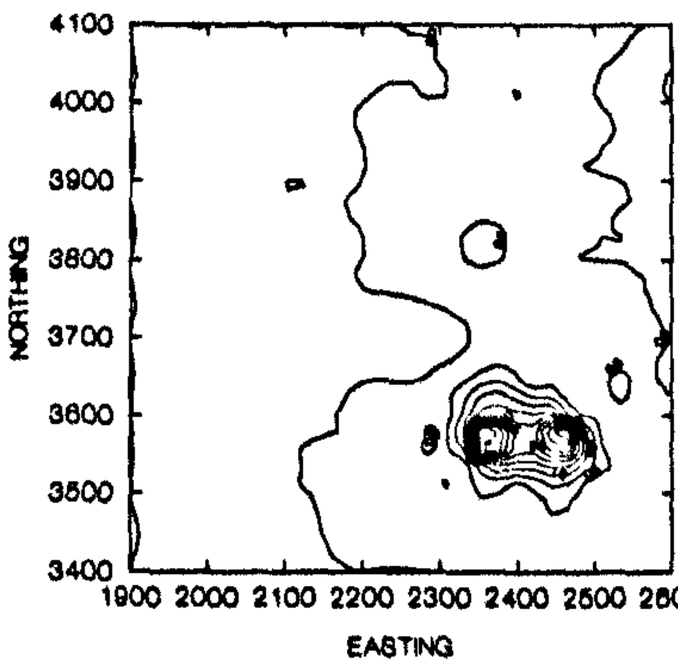
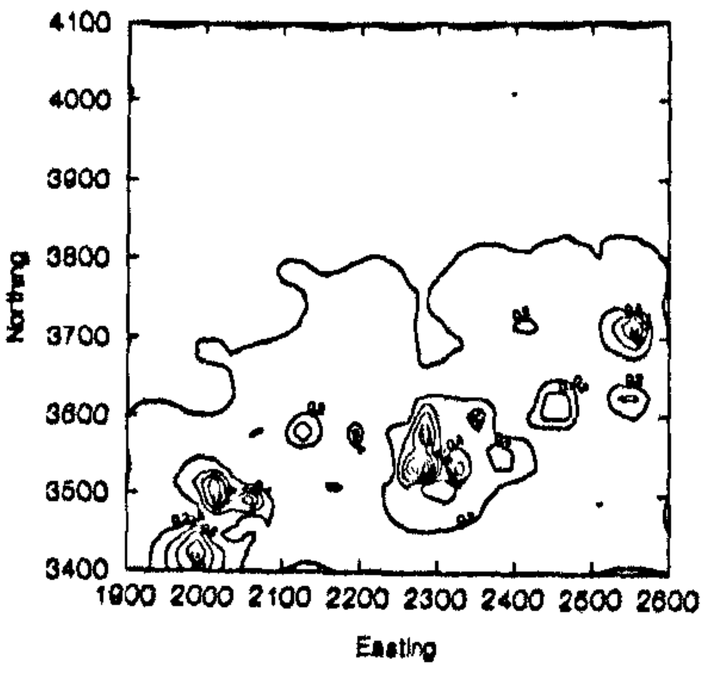
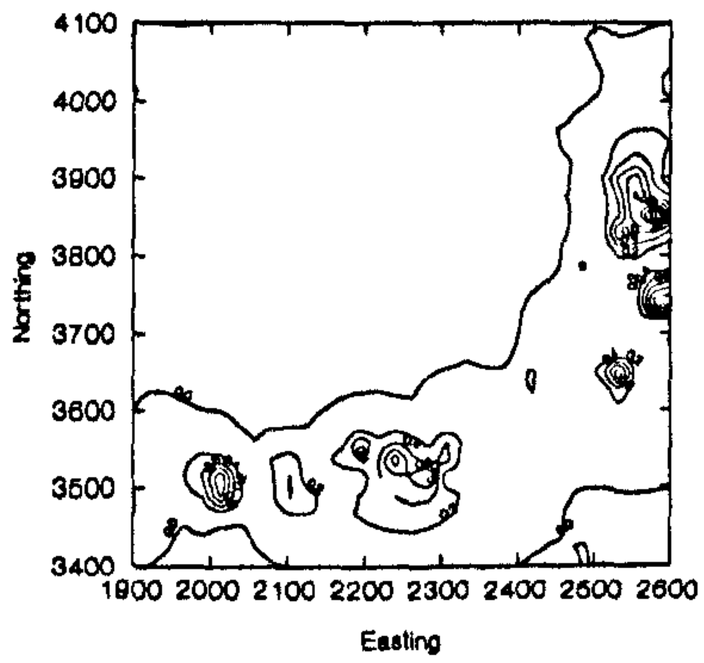


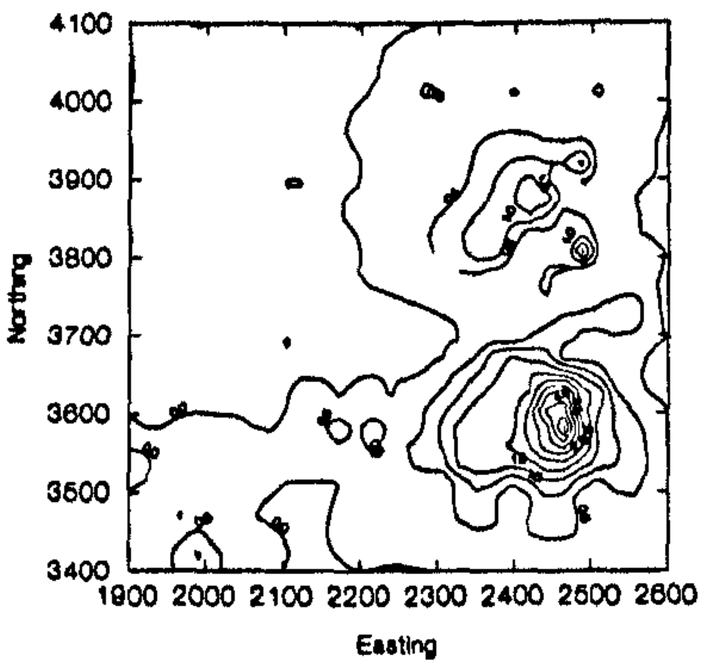
Small copper 1995



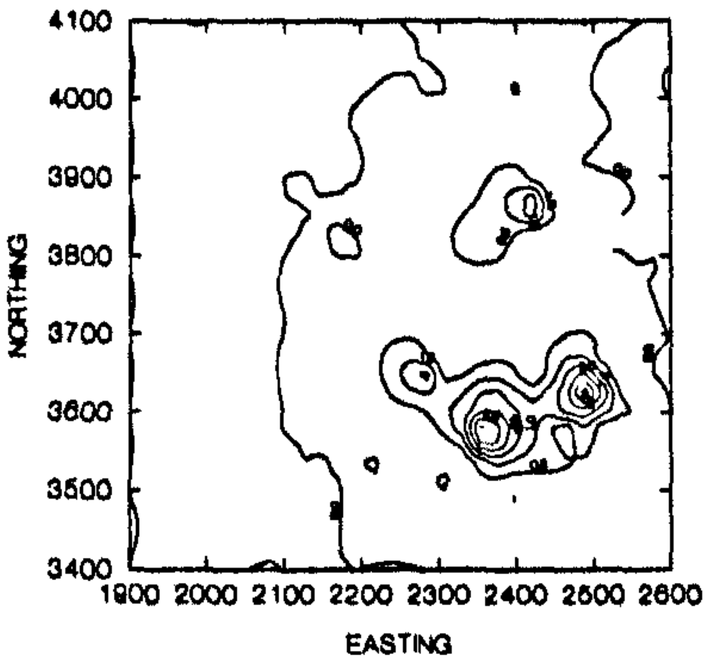
Small blue 1995



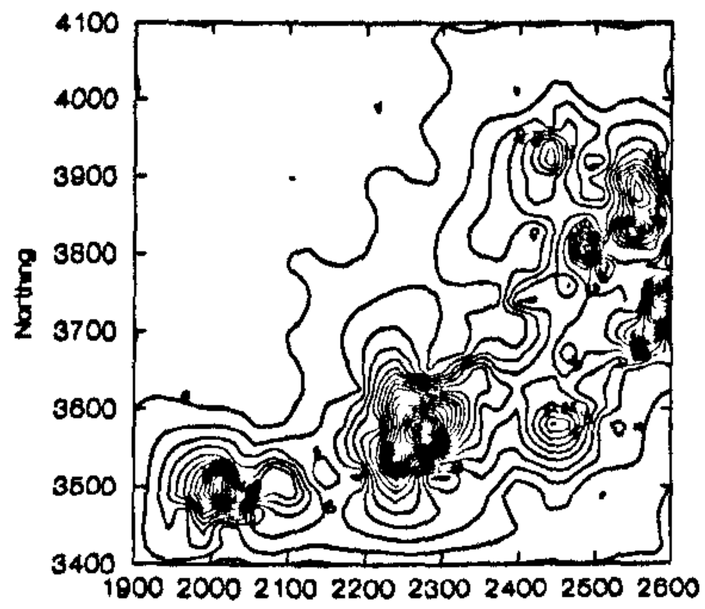
Brown argus 1995



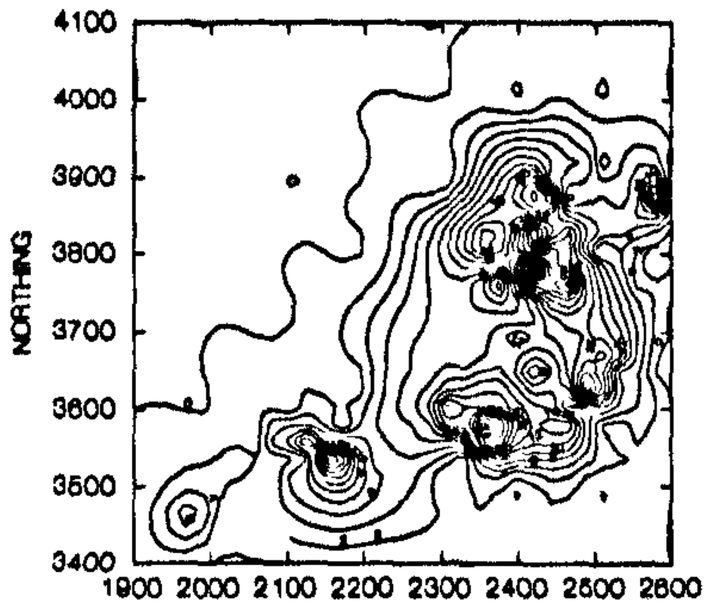
Brown argus 1997



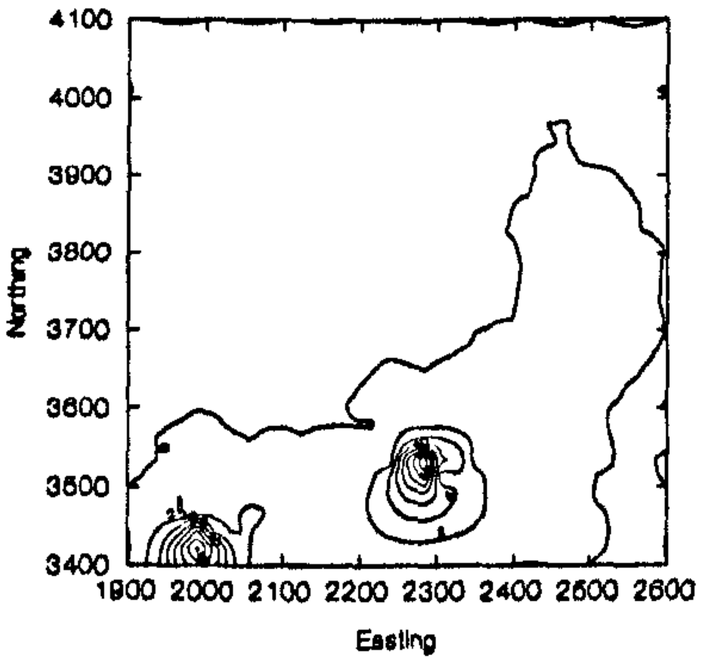
Common blue 1995



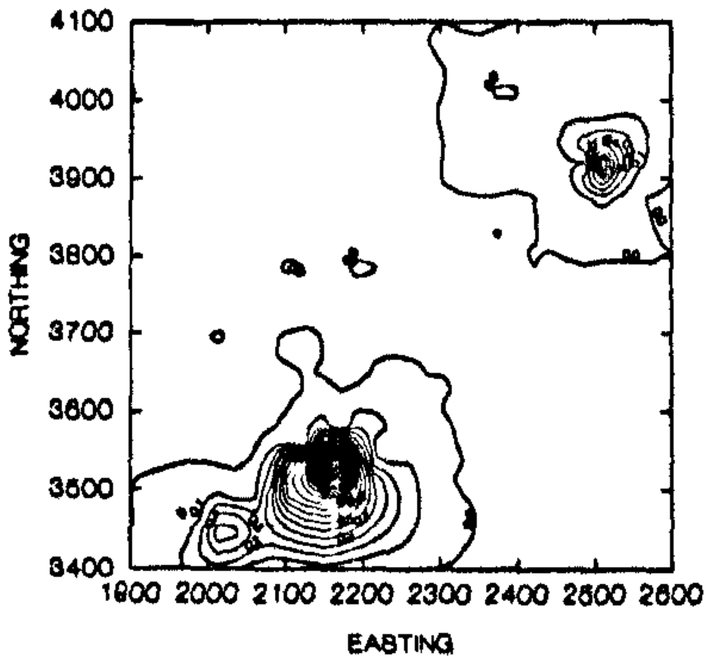
Common blue 1997



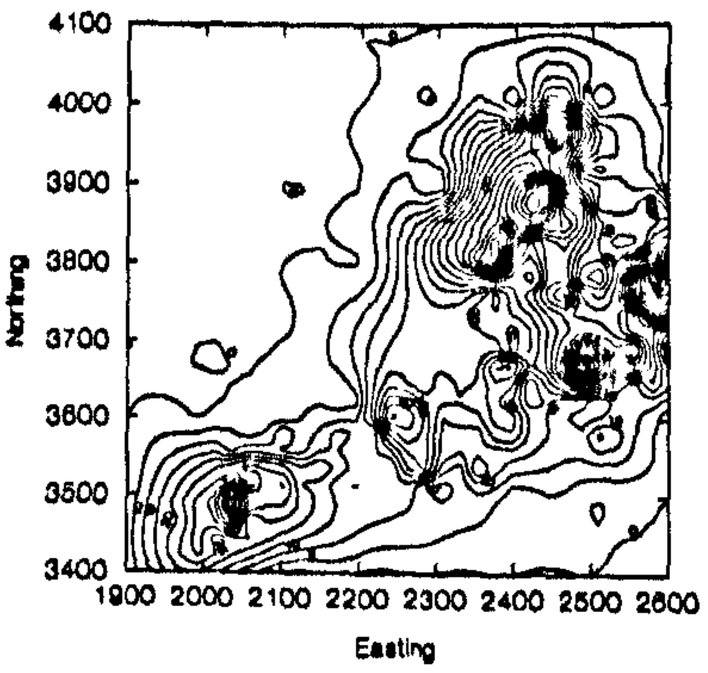
Chalkhill blue 1995



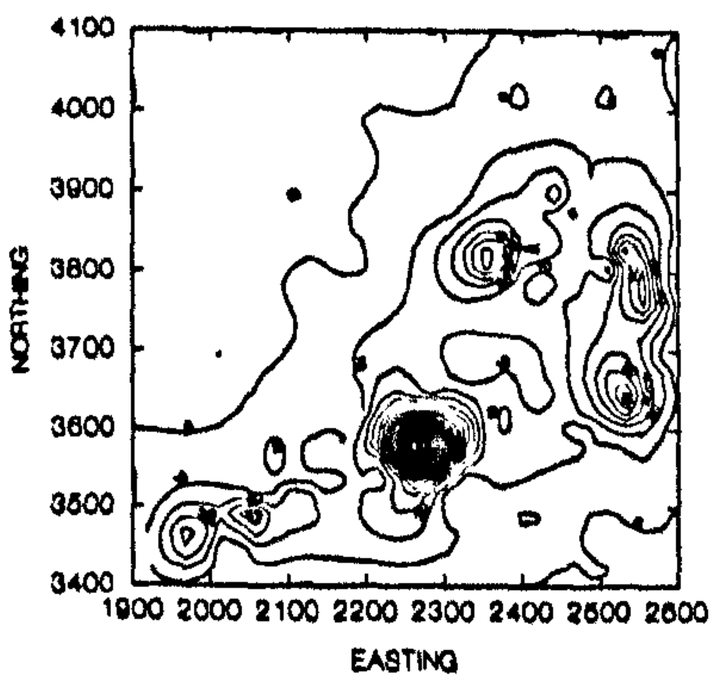
Chalkhill blue 1997



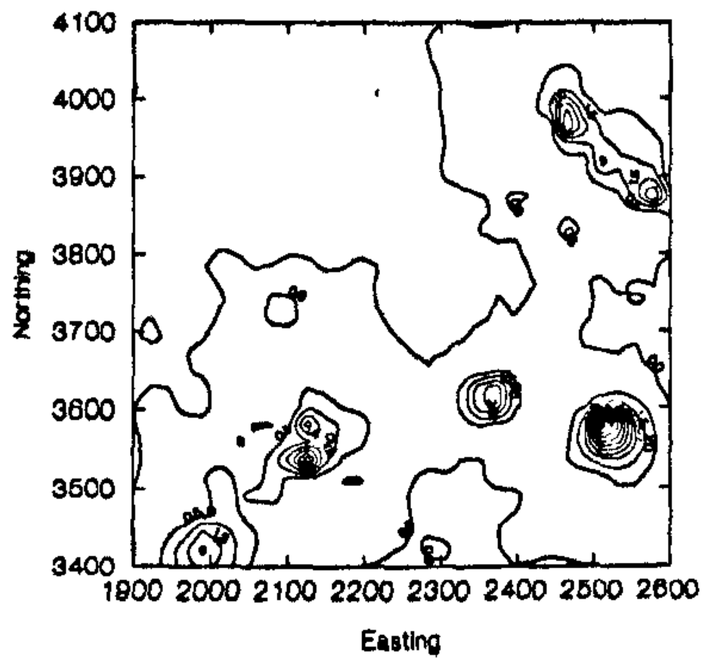
Dark green fritillary 1995



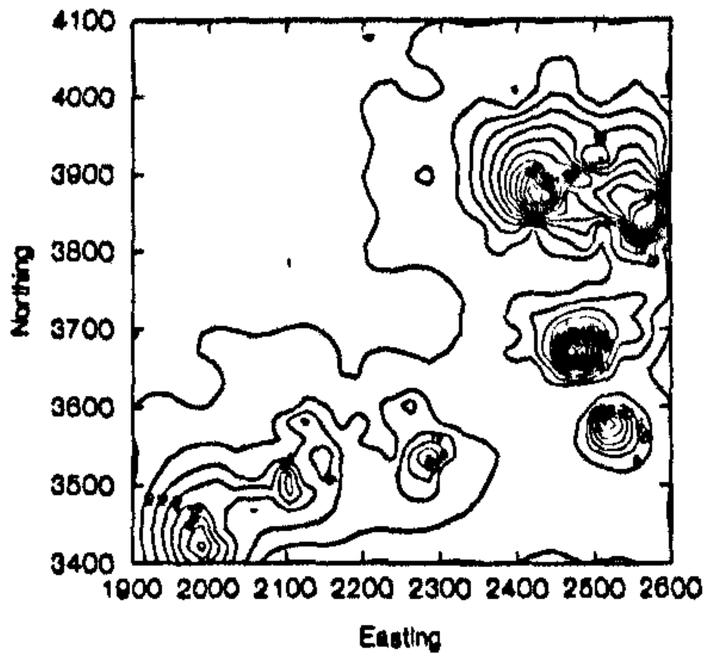
Dark green fritillary 1997



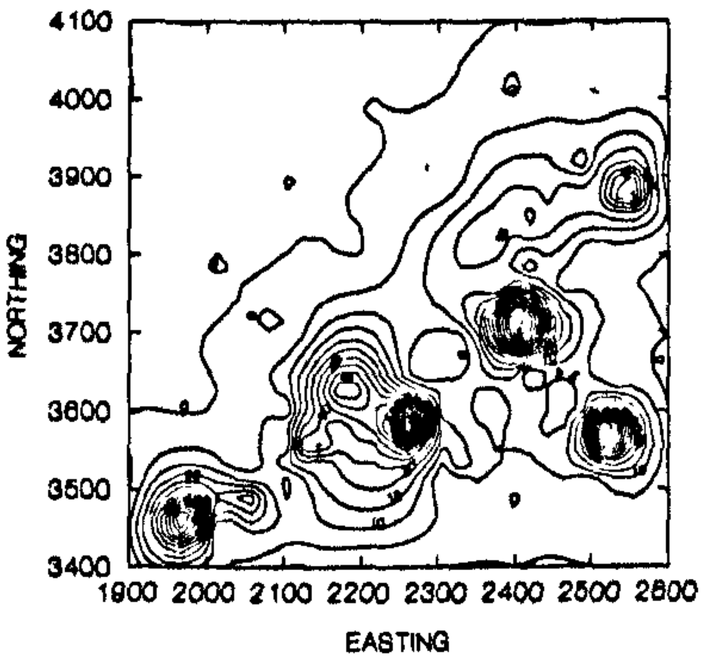
Marbled white 1995



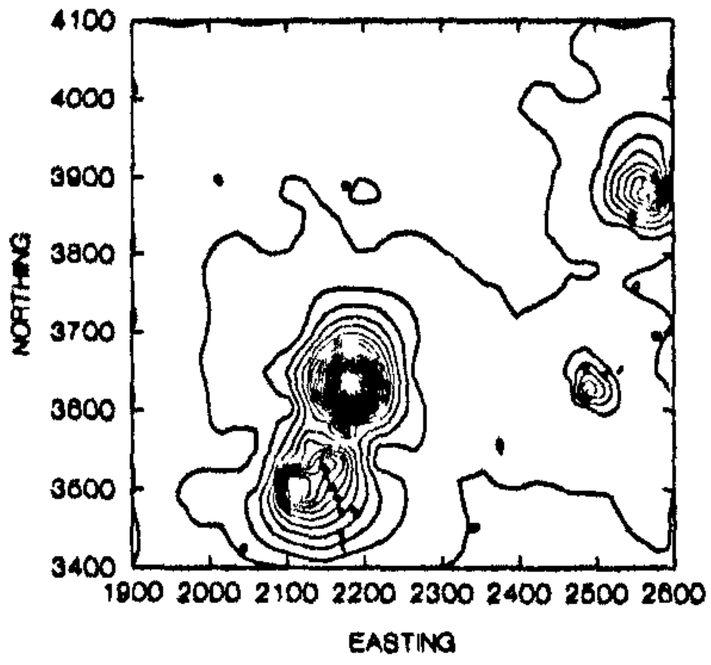
Marbled white 1997



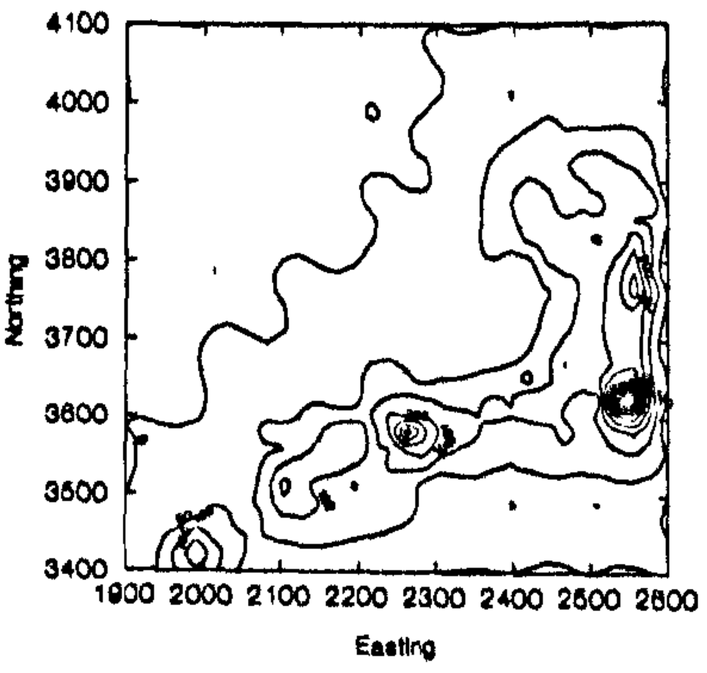
Hedge brown 1995



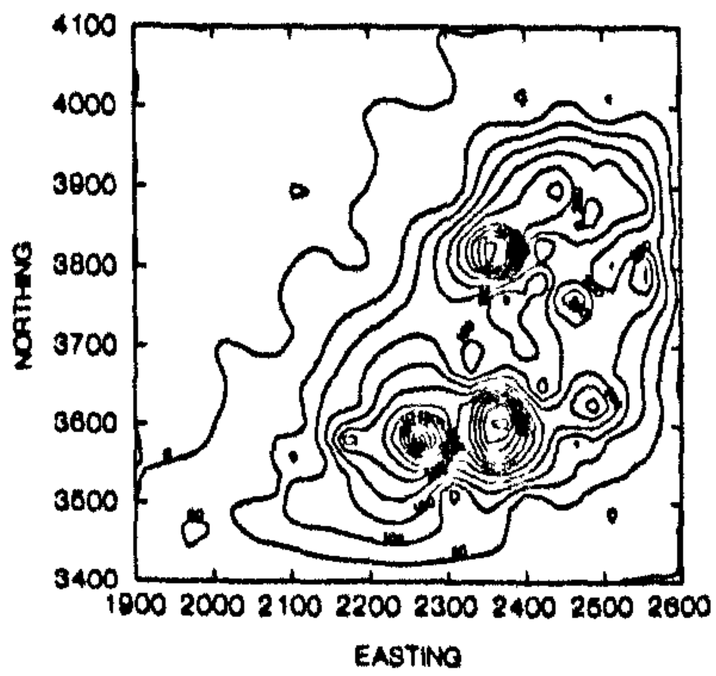
Hedge brown 1997



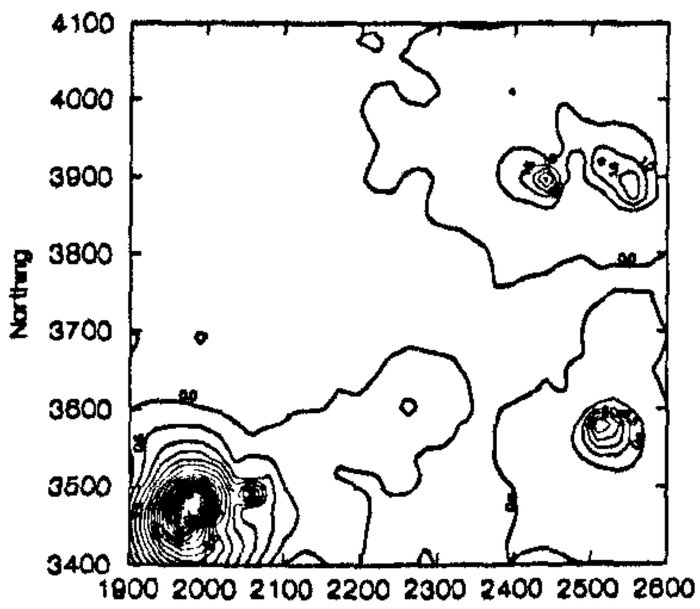
Meadow brown 1995



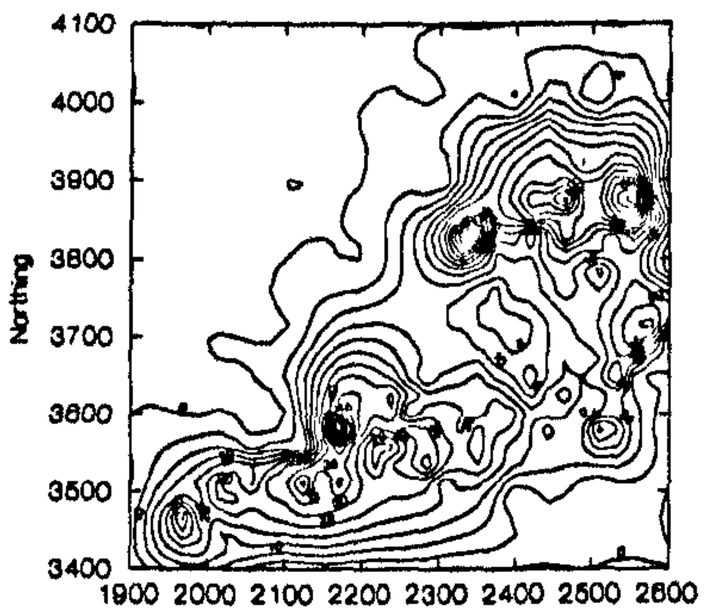
Meadow brown 1997



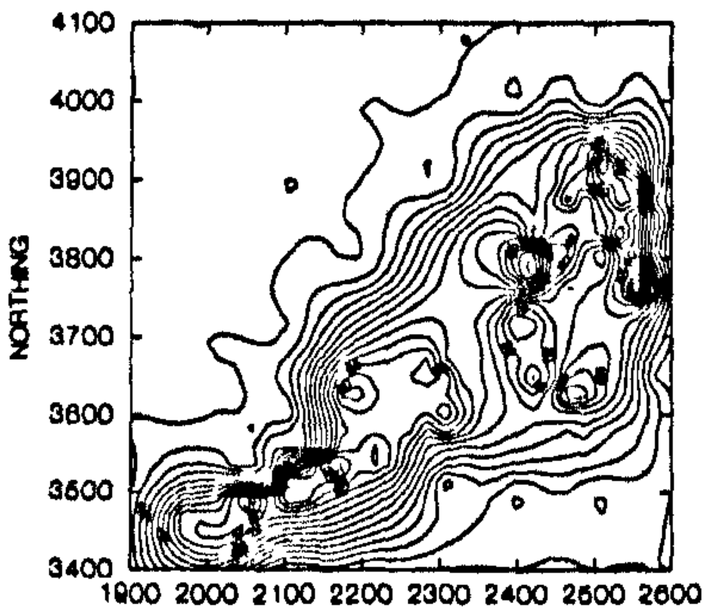
Ringlet 1995



Small heath 1995



Small heath 1997



APPENDIX 8: Intra-set Correlations (Pearson's r) for the Major Data Sets

There are three high correlations (r >0.5) which cause concern. The threshold of r > 0.5 is an arbitrary one but agrees with those used by other workers (e.g. Fielding and Howarth, 1995). The variables involved are sward height, rabbit index, scrub, bare and stones. Of these, the correlation between bare and stones is particularly high.

Appendix 8.1: (Porton Down 1995)

	Sward height	Rabbit index	Aspect
Sward height	1.000		
Rabbit index	-0.558	1.000	
Aspect	0.005	-0.054	1.000
Slope	-0.25	0.240	-0.250
Scrub	0.115	-0.009	0.054
Bare	-0.545	0.297	-0.118
Stones	-0.396	0.264	0.029

	Slope	Scrub	Bare	Stones
Slope	1.000			
Scrub	-0.063	1.000		
Bare	0.038	0.078	1.000	
Stones	0.010	0.067	0.724	1.000

Appendix 8.2: (Porton Down 1997)

	Sward height	Rabbit index	Aspect	Slope
Sward height	1.000			
Rabbit index	-0.445	1.000		
Aspect	0.029	0.006	1.000	
Slope	-0.296	0.257	-0.158	1.000
Scrub	-0.07	0.204	0.311	0.121
Bare	-0.527	0.62	0.171	0.119
Stones	-0.277	0.463	0.328	0.196

	Scrub	Bare	Stones
Scrub	1.000		
Bare	0.343	1.000	
Stones	0.287	0.647	1.000

Appendix 8.3: (Fragmented Sites 1996)

	Sward height	Rabbit index	Aspect	Slope
Sward height	1.000			
Rabbit index	-0.303	1.000		
Aspect	0.054	-0.035	1.000	
Slope	-0.113	-0.091	-0.396	1.000
Scrub	0.174	0.041	0.086	-0.106
Bare	-0.511	0.065	0.074	0.223
Stones	-0.225	0.069	0.119	0.200

	Scrub	Bare	Stones
Scrub	1.000		
Bare	0.176	1.000	
Stones	0.101	0.750	1.000

From these tables, the highest correlations are bare*sward and bare*stones for both the 1997 Porton Down and Fragmented Sites data sets.

APPENDIX 9: Validation of Research Transect Estimation Method

Method

Two BMS-type transects were walked weekly (as per Pollard & Yates 1993) from April-September inclusive during 1995. The transects were located approximately 2km apart but within the same large grassland/scrub/woodland block at Porton Down. Transect 1 (the official ECN/BMS transect) had 15 sections while transect 2 had 12 sections. Transect 2 had several open grassy woodland ride sections plus wood/scrub edge while transect 1 had more open scrub/grassland with several wood edge sections.

Data from transect 2 were used to construct a meadow brown population curve. Each section of transect 1 was used to model section populations using randomly selected sample dates during the flight period using the method above. Two estimates were made from each of one, two, three and four sample dates. Results from estimates were regressed against known BMS indices for each section. The results are shown below.

No. samples during flight period	R^2 values for estimates v BMS section index (regression slope)
1	0.307-0.401 (0.479-0.595)
2	0.503-0.691 (0.537-0.686)
3	0.585-0.943 (0.56-1.07)
4	0.942-0.957 (1.058-1.061)

Conclusions

The best estimates (highest R^2 values and slopes nearest to 1.0) were from three or four samples where samples were drawn from around the peak of the population curve.

Clearly, this method can only be used for commoner species which show a high degree of synchronicity with emergence dates, population peaks and population senescence.

APPENDIX 10: Relationship Between Weekly BMS Indices at Porton Down and Other Sites

Methods

Weekly BMS-type transect data were available for the two transects at Porton plus Broughton Down (approximately 3 km from Porton Down), Dean Hill (approximately 9 km from Porton Down), and Martin Down (approximately 20 km from Porton Down). Weekly indices from sites where counts were considered high enough, were regressed against weekly indices from Porton Down. Indices were log-transformed (ln(index +1)), and linear regression analysis was performed.

Results

Marbled white

The relationship between Porton Down and Broughton Down weekly indices was highly significant (R^2adjusted = 0.935; $F_{1,5} = 87.924$, $P << 0.001$). However, neither relationships between Porton Down and Dean Hill nor Martin Down were significant (R^2adjusted = 0.343; $F_{1,5} = 2.606$, $P = 0.167$ and R^2adjusted = 0.293; $F_{1,5} = 2.074$, $P = 0.209$ respectively).

Hedge brown

The relationship between Porton Down and Broughton Down, Dean Hill and Martin Down weekly indices were all significant (R^2adjusted = 0.903; $F_{1,4}$ = 47.52, P = 0.002, R^2adjusted = 0.755; $F_{1,4}$ = 16.398, P = 0.015 and R^2adjusted = 0.631; $F_{1,4}$ = 9.55, P = 0.037 respectively).

Meadow brown

The relationship between Porton Down and Broughton Down weekly indices was highly significant (R^2adjusted = 0.896; $F_{1,9}$ = 86.756, P << 0.001). The relationship between Porton Down and Martin Down weekly indices was also significant (R^2adjusted = 0.296; $F_{1,11}$ = 6.043, P = 0.032) but the one with Dean Hill was very poor (R^2adjusted = 0.0; $F_{1,11}$ = 0.072, P = 0.794).

Common blue

The relationship between Porton Down and Broughton Down weekly indices was not significant (R^2adjusted = 0.0; $F_{1,16}$ = 0.95, P = 0.344). However, the relationship between Porton Down weekly indices and both those of Dean Hill (R^2adjusted = 0.317; $F_{1,15}$ = 8.417, P = 0.011) and Martin Down (R^2adjusted = 0.336; $F_{1,15}$ = 9.098, P = 0.009) were significant.

The discrepancies in the common blue appeared to be due to differences in the levels of first generations which were relatively much higher at both Porton Down transects.

Conclusions

Apart from hedge brown, which showed synchronous population curves across all sites, the picture is rather mixed as to whether there is enough correlation in population curves for the method to be applied without misgivings. It is known that hedge brown is one of the species whose time of emergence is largely related to day length and would therefore tend to show greater synchronicity across entire regions (Warren, 1992). Other species, including meadow brown, appear to show sensitivity to temperature in relation to emergence time. This would tend to cause local and regional variations in population curves.

Roberts *et al* (1998) and Pearman *et al* (1998) used a method developed by Thomas (1983b) for calculating butterfly populations in study plots from central 'reference' population curves drawn from BMS transects. These curves showed differences among local emergence and peak times of up to seven days, but were felt to be correlated strongly enough by these workers to use in these calculations. Some of these sites were many tens of kilometres apart.

Given that there was an unknown measure of error in using independently obtained weekly indices across sites (not knowing the actual dates of surveys and therefore having potential comparisons up to seven days apart) and the poor data sets from Dean Hill in particular, it would appear that there is enough evidence of synchronicity across the study area for the method to be applied.

APPENDIX 11: Transects Sampled on Porton Down Between 1995 and 1997 and Sampling Periods

1995

	Survey Period				
No Transects	1	2	3	4	5
1-152 incl	1/5-23/5	26/5-14/6	15/6-23/6	26/6-19/7	24/7-14/8
	6				
132	16/8-21/9				

1996

	Survey Period		
No Transects	1	2	3
60	7/5-12/6	12/6-15/7	16/7-19/8
	4		
41	19/8-16/9		

1997

	Survey Period			
No Transects	1	2	3	4
72	30/4-9/6	9/6-11/7	18/7-15/8	15/8-18/9